The history of species concepts and species limits in ornithology

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INTRODUCTION

At all times during the history of modern science, ornithologists contributed to the discussion of general biological concepts based on an exceptionally large amount of information that scientists and collectors had assembled from accessible and remote parts of the world. One such notion is the 'species', the basic unit in the systematic hierarchy of nature. The seemingly endless debate about the species problem over the last 200 years (Mayr 1957, 1982) has been fuelled and at times led by ornithologists. After a period of moderate stability around the middle of this century, the debate has gained momentum during the last 20 years. Therefore, a brief review of the history of the debate within ornithology would seem appropriate. I restrict my discussion to the period after ornithology had emerged as a separate scientific discipline during the first decades of the 19th century (Farber 1982), thus disregarding the important contributions of Ray, Linnaeus, Buffon, Kant, Cuvier and several other early scientists who laid the foundations of later work (Mayr 1982).

During the early stages of the debate, differences of opinion regarding the nature of species often reflected basic attitudes toward the concept of evolution. After the mutability of species in space and their transformation in time through the branching of phylogenetic lineages had been established beyond reasonable doubt, the debate about species shifted to another level. In current discussions, the term species refers to several quite different biological phenomena of evolutionary patterns and processes thereby leading to continuing arguments among the proponents of different concepts and preventing an agreement being reached.

In an introductory section, I present a brief overview of the various theoretical species concepts and of the different taxonomic species categories proposed. These topics have, of course, been the subject of a vast literature of which some titles will be mentioned below. In the main historical chapters, I follow several research trends in the development of species concepts among ornithologists and summarize several estimates of the changing numbers of bird species of the world.

SPECIES CONCEPTS

The species concept—the theoretical idea of the species—is a part of basic biological theory. During the early 19th century and before, the species concept was associated with theoretical ideas of typological essentialism and after Darwin, the species concept was part of evolutionary theory, e.g. the biological species concept as elaborated on by Mayr (1942, 1963). This species concept applies only to sexually reproducing organisms and it is truly valid only in nondimensional situations where species are sympatric or in parapatric contact. Historical 'species' concepts of cladists and palaeontologists refer to phyletic lineages rather than species.

The species as a theoretical notion (concept) needs to be distinguished from the species category within taxonomy to which actual species taxa are assigned (Mayr 1963). The taxonomic species category is, of course, based on the theoretical species concept, but it is a heuristic notion used to order the observed diversity in nature. The taxonomic species categories under different theoretical species concepts have been defined by different authors within narrow, intermediate and wide limits. The intermediate taxonomic species category under the theoretical biospecies concept is Mayr's (1963) multidimensional species category. The distinction between the theoretical species concept and the narrow to wide species category in taxonomy is reflected in the title of this article on species concepts and species limits. The much discussed 'species problem' refers to (1) the application of different theoretical species concepts and (2) the varying methods of delimiting species taxa, i.e. their assignment to differently delimited species categories in taxonomy. The main species concepts may be briefly characterized as follows (Mayr 1942, 1963, 1969):

MORPHOLOGICAL SPECIES CONCEPTS

Species are distinguished from other species and separated from subspecies (geographical 'varieties') on the basis of "degrees of morphological character differences" (rather than distinctness) and, in most cases, the fertility of conspecific individuals (rather than the isolation from nonconspecific populations). Ornithologists emphasizing the diversity of nature and applying a narrowly defined species category in taxonomy (i.e. circumscribing narrow species taxa) have been characterized as 'splitters'; others define the taxonomic species category more widely and emphasize the transitional nature of intergrading taxa and include wider arrays of geographically representative forms in more heterogeneous species taxa ('lumpers'). We may contrast a non-evolutionary (pre-Darwinian) and an evolutionary (post-Darwinian) concept of morphospecies. Species were assumed to possess certain constant features considered as "more essential" under the former view and "more primitive" under the latter viewpoint.

Non-evolutionary morphological concept. Under this theoretical species concept, the organic diversity reflects the expression of underlying 'types' and the observed variation is the result of different manifestations of the 'type'. This concept is typological, creationist and basically non-evolutionary.

Evolutionary morphological concept. Although the transformation of species and the branching evolution of organisms are accepted under this concept, species and subspecies are separated exclusively on the basis of morphological character differences and, in many cases, the fertility of conspecific individuals. Basically, this is the species concept of Charles Darwin in his *Origin of Species* (1859; not during the late 1830s) and of many zoologists during the late 19th into the 20th centuries.

This theoretical concept in a sense is transitional between the typological and biological species concept. W. Bock (pers. comm.) pointed out that, ultimately, it may not be possible to make a distinction between authors who accept an "evolutionary morphological species concept" and those who accept a "biological concept" but just use morphological differences to recognize different species taxa or make the distinction between what taxa are considered species and subspecies. Even today if one uses the biological species concept and the fundamental criterion of no genetic exchange between species, species taxa are recognized almost entirely on the basis of morphological differences between members of various species. Also individual organisms are identified as members of a particular species on the basis of morphological similarity. Although this is true, I feel there is a conspicuous difference between the theoretical views of authors who search for intrinsic, qualitatively different morphological characters of species (*versus* subspecies) and those who have the understanding that there is no intrinsic difference between the characters of species and subspecies and who just use morphological characters as indicators for geneflow actually or potentially to take place.

BIOLOGICAL SPECIES CONCEPT

"Species are groups of actually (or potentially) interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1942, 1963, 1969). Reproductive isolation is usually understood to mean genetic isolation, e.g. "possession of a shared genetic program is the common tie uniting individuals derived from the gene pool of a given species" (Mayr 1968: 164). Bock (1986) made this explicit by emending the definition to read "a species is a group of actually or potentially interbreeding populations of organisms which are genetically isolated in nature from other such groups". This emendation appears useful in view of the discovery in recent decades of several cases of representative taxa, especially of insects, that hybridize freely along the contact zone because of the lack of premating isolating mechanisms, but in which such cases hybrids are infertile because of fully developed postmating isolating mechanisms (parapatric hybridization). Some birds which meet along "zones of overlap and hybridization" (Short 1969) may also represent taxa which are genetically isolated but not reproductively isolated in a strict sense. These biological species would be considered as conspecific under Paterson's (1985) "recognition concept" of species. Panov (1989) and Grant & Grant (1992) reviewed the complex topic of hybridization and introgression in bird species as it relates to ethological isolation and the definition of the biological species border.

A fully differentiated biological species is a genetic unit, a reproductive unit and an ecological unit occupying a species-specific niche in nature (Mayr 1969, Bock 1986); it is capable of living sympatrically with other such species (synspecies—Sudhaus 1984). Taxa which replace each other geographically without or with only very restricted hybridization along the contact zone (paraspecies *sensu* Sudhaus 1984, as well as semispecies *sensu* Short 1969, respectively; see Table 1) are strong competitors owing to the lack of ecological isolation but have reached the level of biological species. It appears inadvisable to include ecological isolation in the taxonomic species definition (Mayr 1982: 273) since this would reduce semispecies and most paraspecies to the level of conspecific entities and would make the zoogeographical species (synspecies) the basic unit of the taxonomic system. Nevertheless, the process of microtaxonomic differentiation is not complete until genetic, reproductive, as well as ecologic isolation have been reached (Mayr 1942, Lack 1944, Bock 1979).

The biological species concept is nondimensional and can be applied readily (directly) only to sympatric or parapatric populations. It is the multidimensional species notion in taxonomy with its extensions over space and time which applies to most real units observed in nature, the species taxa, and which are subject to all the difficulties of any pragmatic application of theoretical concepts (Mayr 1963, 1982, Bock 1979, 1986). The distinctiveness of species becomes increasingly vague as one progresses geographically and chronologically further and further away from a single point where 2 species occur in sympatry or parapatry. The species category as a part of the taxonomic hierarchy should be defined broadly as the multidimensional species notion (many authors, however, applied fairly narrow limits to their taxonomic species category). Moreover, this category should be sufficiently broad and pragmatic to include species taxa of nonsexually reproducing organisms. We should also realize that it may well not be possible to formulate a single multidimensional species notion which is applicable to all known organisms.

On continents, intergradation of contiguous populations or their geographical exclusion without hybridization along the contact zone determines their rank as subspecies and paraspecies, respectively. Allopatric populations are assigned subspecies or species status on the basis of

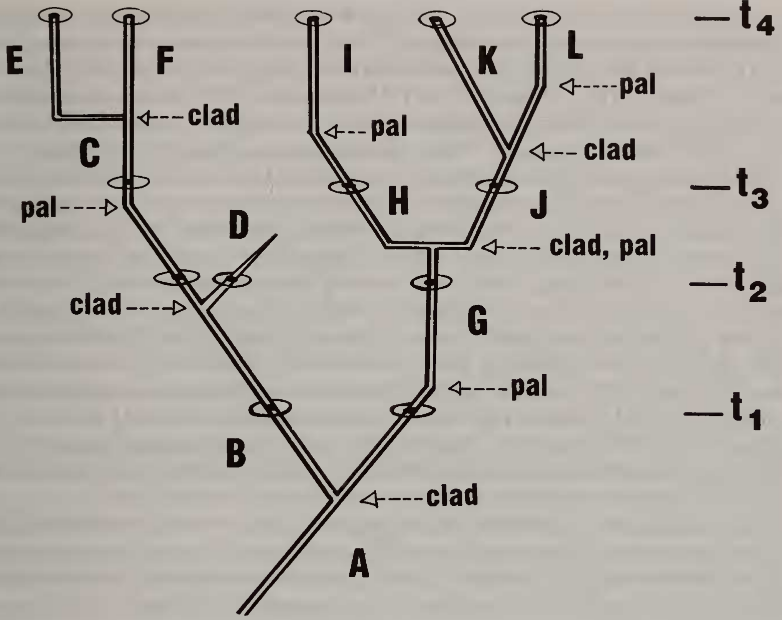

Figure 1. Several imaginary phylogenetic lineages to illustrate 'species' limits under the cladistic concept (clad.) and the palaeontological concept (pal.). Schematic representation. Groups of populations representing the various lineages at particular time levels (e.g. t_1–t_4) are different biological species (oval circles). Vertical scale—geological time; horizontal scale—morphological and other biological changes. A–L represent palaeontological 'species', except C–F, which together are one palaeontological 'species' but represent 2 cladistic 'species'.

inference (Mayr 1969: 197). For example, the Serin *Serinus serinus* and the Canary *Serinus canaria* were considered allopatric species because of their conspicuous differences in colour, shape of the bill and song which were interpreted as potential isolating factors. The Serin has invaded the Canary Islands in recent years, where it now lives sympatrically with *S. canaria* on several islands thus demonstrating its specific distinctiveness (which, of course, it had possessed already in allopatry, although unchallenged).

It may be advisable in the future to establish a scale for labelling species taxa by a number or a symbol according to the estimated reliability of their delimitation. Species taxa consisting exclusively of well differentiated allopatric subspecies or several monotypic species on islands would be low on this scale, whereas more widespread monotypic species on continents as well as polytypic species consisting of directly intergrading subspecies would be high on this 'reliability scale'.

The 'horizontal' concept of the biospecies (Fig. 1) refers to genetically isolated reproductive communities of a particular time level such as the Recent period or any other time level of the geological history of the earth (Peters 1970, Bock 1979, 1986). The vertical extent ('thickness') of such a geological time 'level' ('slice') or in other words the "duration" of a species is a matter of convention and, in most cases, will be determined by the incompleteness of the fossil record. The term 'chronospecies' has been used for artificially delimited and fairly extensive portions of phylogenetic species lineages (e.g. Remane 1985, Willmann 1985). Anagenetic change of a phylogenetic lineage through time does not signify 'speciation', which term refers here exclusively to the phenomenon of lineage splitting.

Morphologically differentiated taxa which merge through broad or narrow hybrid zones are combined as subspecies and megasubspecies of one biological species (Amadon & Short 1976 and in this volume). Admittedly, this procedure fairly frequently subsumes under one species name, and thus 'conceals' at that intermediate level, 2 or more conspicuously differentiated entities with independent biogeographical histories. A biogeographical species (Mayr & Short 1970, Bock & Farrand 1980, synspecies—Sudhaus 1984) comprises a superspecies or an independent biological species (which is not a member of a superspecies). Biogeographical species represent communities of descent and are the highest taxa which, on the basis of the genealogical relations and allo/parapatric distribution patterns of the component forms, can be delimited objectively (Rensch 1934: 51, Mayr 1942: 169).

The distribution patterns of groups of closely related parapatric biospecies resemble large scale mosaics composed of neatly interlocking patches formed by the ranges of the component species. Parapatric and allopatric biospecies are combined in a superspecies if they "... were once races of a single species but which now have achieved species status" (Amadon 1966, 1968). Geographically representative and closely related species are included in a superspecies even if their ranges overlap to a certain extent and the width of overlap is narrow relative to the vagility of taxa involved and the respective total ranges occupied (the amount of overlap is undefined). Component biospecies of superspecies have been designated paraspecies (Prigogine 1980, 1984a,b, Sudhaus 1984) if they are in contact, restricting the term allospecies (Amadon 1966) to geographically separated representatives. In some groups of animals parapatry probably persists long after the respective populations have attained genetic isolation and not only one but 2 or more speciation events have taken place (Haffer 1986).

Cladistically, the representatives of a superspecies are in most cases each others' closest relatives because of a basically consistent association between character evolution, genetic-reproductive isolation and ecological differentiation. However, detailed analyses may reveal that this is not true in some cases when one of the representatives of a superspecies is the sister taxon of another widely sympatric species. It remains to be determined how frequent such situations actually are. Selander (1971), Vuilleumier (1976) and Mayr (1980b) discussed various general aspects and problems of the application of the biological species concept to the avifaunas of the world.

The informal term 'species group' refers to a group of closely related species with extensively overlapping ranges (Mayr 1963; ex-superspecies—Vuilleumier 1985). These species have attained reproductive-genetic isolation from and ecological compatibility with each other; they are fully biologically compatible.

HISTORICAL "SPECIES" CONCEPTS

'Vertical' species concepts here combined under the designation 'historical' concepts or 'phylogenetic concepts' refer to portions of a phylogenetic lineage in time (Fig. 1). A 'vertical' lineage, however, represents an evolutionary phenomenon quite different from the notion of the 'horizontal' biological species discussed above (Bock 1979, 1986, Gittenberger 1972). A separate nomenclature and taxonomic system should be conceived to deal with phyletic lineages. The phyletic lineage is the continuum of a species as its members reproduce generation after generation through time. The phenotypic characteristics of the members of a phylogenetic lineage, and hence the underlying genetic bases, may remain the same over long geological periods (stasis) or change more or less gradually through time (phyletic evolution). A phyletic lineage may remain undivided over long periods or it may split (speciate) into 2 or more separate phyletic lineages from time to time (Bock 1986, Reif 1984). As Bock (1986: 38) and Szalay & Bock (1991: 15) have stated "A cross-section of a phyletic lineage at any point in time is a species (theoretical, non-dimensional). However, different time slices through the same phyletic lineage are not different species, nor are they the same species. They are simply different cross-sections of the lineage at different times, with the earlier one being ancestral to the later one. Each time slice is a species, but it makes no sense to ask whether they are the same or different species; the question lies outside the theoretical, nondimensional species concept and hence, from a theoretical perspective, is a non-question." In this sense a species has no origin, life span or age. The species populations of a phyletic lineage through time often altered their morphologies drastically at different time levels (phyletic evolution) and their biological relations to other contemporary species changed completely. No species boundary can be meaningfully placed along such a continuous lineage undergoing a rapid evolutionary shift or in the case of a branching lineage.

Of course, all phyletic lineages need to be studied in detail as they are important entities of the evolutionary history of a group of animals but, in contrast to species, they are not involved in the processes of evolution, i.e. phyletic evolution and speciation, which take place in living populations. Phyletic lineages "are the time paths (the record) resulting from the outcomes of these processes in species taxa. Phyletic lineages are history and as such are not involved in the ongoing process of evolutionary change; they do not have a role in the process itself. Species, not lineages, evolve and thereby have the proper claim to the attention of workers interested in the processes of evolutionary modification. Phyletic lineages have the proper claim for the attention of workers interested in analyzing the historical course of life" (Szalay & Bock 1991: 16). In their conclusion, these authors emphasize that "unless evolutionists and taxonomists make a clear distinction between these dual concepts (the species and the phyletic lineage), no hope exists to resolve the endless discussion on the ontology and epistemology of the species". The conceptual difference between the species of neontologists and the chrono-"species" of palaeontologists has been discussed by several other authors previously (e.g. Mayr 1942: 154, 1982: 292, Simpson 1961, Peters 1970, Bock 1979, Remane 1985).

The differences between the 2 historical "species" concepts refer to a different delimination of "species" as portions of phyletic lineages (Fig. 1). I designate Simpson's (1961) concept as "palaeontological" and the concept of Hennig (1950, 1966) as "cladistic". The designation 'evolutionary species' for the palaeontological concept is ambiguous, as this name has been applied also to certain cladistic concepts in recent years.

Palaeontological "species" concept. Palaeontologists, beginning with Simpson (1951, 1961), defined the species as follows: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." Under this concept, species limits may or may not coincide with speciation events, i.e. branching of lineages.

Cladistic "species" concept. Hennig (1966: 59) considered a species as a phyletic lineage between 2 successive speciation (branching) events or until the lineage terminates (see also Willmann 1985). Character change may or may not occur in the 2 daughter species. Other definitions are "A species is a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind" (Eldredge & Cracraft 1980: 92) or "Species are simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters" (Nelson & Platnick 1981: 12) and "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" ("*phylogenetic species*"— Cracraft 1983: 170). Cracraft and other cladists delimit "species" narrowly to be certain that these taxa are monophyletic, whereas Hennig (1966), Willmann (1983, 1985, 1986) and others apply the concept of monophyly only to groups of species. Accordingly, the latter authors delimit species more widely (as is done under the biospecies concept). Donoghue (1985) and Mishler & Brandon (1987) also proposed a "phylogenetic species concept" which, besides a grouping component (monophyly in the cladistic sense), recognizes a ranking component (e.g. interbreeding, selective constraints, or strong developmental canalization). This leads to narrow or broad delimitations of species taxa. According to most cladists, the life of an ancestral "species" ends when it splits into 2 new "species". Wiley (1981: 35), however, does permit the budding off of a "species" from another one which survives the speciation event. See further discussions of cladistic "species" concepts by Frost & Hillis (1990) and by several authors in *Cladistics* 5 (1989) and 6 (1990).

SPECIES LIMITS

Under each of the theoretical species concepts mentioned above, zoologists delimited and are delimiting 'narrow' or 'wide' species taxa depending on the placement of the species limit at 'low' or 'high' levels of microtaxonomic differentiation, respectively. In other words, based on each theoretical species concept, systematists devised differently conceived (wide to narrow) heuristic species categories in taxonomy used to order the observed diversity in nature. A species limit at a fairly high level of differentiation results in relatively few species taxa with each species comprising wide arrays of variously differentiated geographical representatives, whereas a species limit at a low level of differentiation results in more numerous, rather uniform, narrowly defined species taxa.

Following Mayr (1942, 1963), Lack (1944, 1971), Short (1969, 1972), Bock (1979, 1986) and others I have schematically subdivided the process of microtaxonomic differentation into 6 stages (Table 1). Each of the intermediate levels between one fairly uniform species (stage 1) and 2 fully biologically compatible synspecies (stage 6) are represented in the world's avifaunas by differentiated bird populations in contact. These stages are here listed in a presumed temporal sequence of gradually increasing microtaxonomic differentiation. Aspects of behavioural differentiation between closely related forms are subsumed under "genetic isolation" (e.g. differing types of song) and/or "ecological separation" (e.g. different feeding behaviour) and may be the cause of genetic or ecologic isolation between these relatives. Examples of such behavioural differences are many species of dabbling ducks whose reproductive isolation is maintained through different courtship behaviour and many species of North American warblers (Parulidae) and Holarctic tits (*Parus*) whose coexistence is maintained through different feeding behaviour and different feeding stations in trees.

Table 1 is an attempt at visualizing the process of microtaxonomic differentiation through a schematic grid of increasing levels of morphological, genetic-reproductive and ecological differentiation. The grid and, in particular, the sharp boundaries of the various stages (microtaxonomic categories) are rather crude means of schematically illustrating the results of the differentiation process. Nature is not necessarily orderly and extant faunas provide many examples of taxa at transitional stages between the categories distinguished here or of taxa which combine aspects of 2 categories in different areas of contact (e.g. hybridization occurring in one area of contact and overlap of their ranges to some extent without hybridization in another area of contact). Morphological differences may or may not render a group of populations diagnosable taxonomically at an early stage of differentiation (subspecies). In some bird populations genetic isolation may be completed before ecological segregation from the nearest relative is reached. This situation leads to geographic replacement (parapatry) of these forms when they come into contact (with no or only limited hybridization). The frequent occurrence of superspecies in the avifaunas of the world (Sibley & Monroe 1990) indicates that ecological competition often prevents sympatry of geographical representatives long after speciation is complete (Lack 1944, Mayr 1963). Many species probably perfected ecological segregation and certain aspects of reproductive isolation in neosympatry, but not genetic isolation, which must evolve fully in the initial allopatric period (Bock 1979, 1986, Grant 1986). The process of speciation has terminated only after the differentiating taxa have attained genetic-reproductive *and* ecological separation (leading to sympatry of synspecies). Under the biospecies concept, most authors currently place the limit of the taxonomic species category at level III (Table 1), as discussed by Short (1969,

TABLE 1

Components of microtaxonomic differentiation. Taxa at various stages of increased modification are assigned to collective taxonomic categories listed at right and here named under the biological species concept. Dashed lines indicate the position of the species limit under different taxonomic categories as follows: narrow cladistic 'species' category (I, II), multidimensional species category and broad cladistic 'species' category (III), species category under the recognition concept (IV), biogeographical species category (V)

Stages in the differentiation process		*Relations between taxa along contact zone*	*TAXA* *Level of differentiation reached* Morphological differentiation	Genetic isolation	Reproductive isolation	Ecological separation	*Taxonomic categories*	
6		SYMPATRY	(+)	(+)	(+)	(+)	Synspecies	
								V
5	PARAPATRY	COMPETITION PARAPATRY	(+)	(+)	(+)	–	Paraspecies	
								IV
4		HYBRIDIZATION PARAPATRY OVERLAP & HYBRIDIZATION PARAPATRIC HYBRIDIZATION	(+)	(+)	–	–	Semispecies	
								III
3	HYBRIDIZATION	NARROW HYBRID ZONE	(+)	–	–	–	Megasubspecies	
								II
2		WIDE HYBRID ZONE	(+)	–	–	–	Subspecies	
								I
1		CLINAL VARIATION	–	–	–	–		

(+), Present; –, absent.

1972). Hennig (1966) and Willmann (1985, 1986) also delimit the species category at approximately this intermediate level of differentiation, whereas other cladists (e.g. Nelson & Platnick 1981: 12, Cracraft 1983) delimit the taxonomic species category at the lower levels I or II.

Not all speciating taxa pass necessarily through all stages of the microtaxonomic differentiation process (Table 1). Small founder populations on islands, originating presumably from few individuals and speciating in bottleneck situations during peripatric speciation (Mayr 1982), probably differentiated rather quickly and directly from low to high levels of microtaxonomic modification (mode "Type Ib: speciation by the founder effect"—Bush 1975: 346). On the other hand, many continental species that differentiated through 'splitting' from fairly large isolated populations resulting from fragmentation of an ancestral species range ("Type Ia: speciation by subdivision"—Bush 1975: 341; dichopatric speciation—Cracraft 1984) probably originated more slowly through general genetic transformation (Mayr 1987: 312). Bush (1975: 341) referred to this mode of speciation as "a relatively long-term process". Consequently, taxa at various intermediate levels of microtaxonomic differentiation are comparatively common in continental faunas. The separation of populations leading to peripatric and dichopatric speciation had been designated, respectively, as primary and secondary disjunctions by Hofsten (1916). He showed that the occurrence of these 2 different types of discontinuities was already well-known to Forbes, Darwin, Wallace and other early biogeographers.

ORNITHOLOGISTS AND SPECIES CONCEPTS

During the past 200 years, ornithologists have used the different species concepts discussed above to classify the numerous kinds of birds of the world. Under each theoretical species concept, systematists delimited species taxa within wide, intermediate or narrow boundaries, i.e. they assigned species taxa to differently conceived species categories within taxonomy. From these considerations, I have constructed Table 2 listing the theoretical species concepts along the horizontal axis and subdividing each concept along the vertical axis according to wide, intermediate and narrow limits of the respective species categories in taxonomy. In this Table, I have placed a selective number of ornithologists at a position approximately corresponding to their theoretical viewpoints regarding the species as a theoretical concept (horizontal axis) and as a category within taxonomy (vertical axis). Additional ornithologists are mentioned in the text. Certain aspects of the taxonomic species category applied by a systematist can be deduced from his narrow to wide delimitation of species taxa. On the other hand, his theoretical species notion, i.e. his typological-creationist or evolutionary attitude, is often far less obvious and more difficult to ascertain. Therefore details of the taxonomic species categories applied by ornithologists are treated in more detail in the following pages than details of their underlying theoretical species concepts.

Schematic Table 2 and, in particular, the sharp distinction of the theoretical concepts do not permit an illustration of the numerous

TABLE 2

Theoretical species concepts (horizontal) and species limits under different taxonomic species categories (vertical) as applied by some ornithologists during the 19th and 20th centuries, supplemented by the names of several cladists and palaeontologists. Years refer to major publications; see text for details. Further literature search probably will reveal certain cladistic and palaeontological authors, who delimited species widely or narrowly, occupying the blank boxes of this table.

Species concepts Species limits	1. MORPHOLOGICAL (Concept of "difference")		2. BIOLOGICAL ("Horizontal" concept) The reproductive community	3. HISTORICAL ("Vertical" concepts) The phylogenetic lineage	
	non-evolutionary	evolutionary		cladistic	palaeontologic
Wide	Gloger 1833 Middendorff 1853 Kleinschmidt 1926	Geyr 1924 Meinertzhagen 1954 Eck 1985	Hellmayr 1920s Stresemann 1919–1927		
Intermediate	Schlegel 1844 Blasius 1862	Darwin 1850s Baird 1870s Coues 1870s Allen 1870s Ridgway 1870s Grinnell 1921	Darwin 1830s Seebohm 1880s Hartert 1903–1922 Stresemann 1928 ff. Rensch 1929, 1934 Mayr 1942, 1963 Lack 1944, 1947 Bock 1979, 1986	Hennig 1966 and followers, e.g. Willmann 1985	Simpson 1961 and other palaeontologists
Narrow	Temminck 1815 Vieillot 1816 C. L. Brehm 1823, 1831	Sharpe 1899–1909 P. L. Sclater 1880s Hartlaub 1877 Reichenow 1913	Stepanyan 1974, 1978	Cracraft 1983 McKitrick & Zink 1988	

relations and interconnections between and among the various viewpoints which have certainly existed at all times. In addition, certain authors have not always been consistent in their work, applying to comparable situations sometimes wide species limits and on other occasions intermediate species limits. Despite these difficulties, Table 2 does permit a valid distinction to be made between the basic theoretical views of such well-known authors as, e.g., Sclater, Allen, Kleinschmidt, and others.

Stresemann (1927, 1951, 1975), Rensch (1929b) and Mayr (1942, 1963, 1982) discussed many aspects of the development of ornithological systematics in their wide-ranging studies, in particular regarding the microtaxonomic levels with which I am concerned in this article. Additional historical data have been mentioned by Miller (1955) and Sibley (1955). My emphasis will be on some of those aspects not covered or only briefly discussed in these publications. Biographies of most ornithologists mentioned below have been published by Mullens & Swann (1917), Gebhardt (1964 ff.), Gillispie (1970 ff.) and Means & Mearns (1988).

I am here concerned with the discussion of the species problem by ornithologists. A more comprehensive treatment would need to take also into consideration the interesting contributions of certain botanists, entomologists and malacologists during the 19th century, some of which have been insufficiently appreciated in the recent literature.

MORPHOLOGICAL SPECIES CONCEPTS

Nearly all zoologists of the 19th century applied morphological species concepts. This was the time of intensive geographical and biological exploration of the world. The museum specialists studied numerous animal collections which professional collectors had assembled abroad; most of these systematists placed species taxa in a narrowly defined taxonomic category of morphospecies. Several explorer-naturalists personally made large collections of birds, mammals and insects in the field during extended expeditions. They were able to apply to the study of the collected material their extensive field experiences and arrived at widely circumscribed species taxa (broadly defined taxonomic species category). In addition, they analyzed various general aspects of geographical variation in animals.

Museum ornithologists: narrow species limits

The narrow Linnaean species of many 19th century ornithologists comprised one morphologically defined taxon (a subspecies or a monotypic species in current terminology), frequently described on the basis of only one or two specimens which represented the 'type' of the species (in the sense of the Platonic typological type). Intermediate specimens were dismissed as hybrids possessing no more significance than any abnormal animal. These were the species of many museum workers in Europe, e.g. C. J. Temminck, L. P. Vieillot, R. P. Lesson, C. L. Brehm, H. Lichtenstein, N. A. Vigors, W. MacGillivray, C. L. Bonaparte, W. Swainson, G. R. Gray and others, during the first half of the last century as well as of several leading systematic ornithologists during the late 19th into the early 20th centuries, e.g., J. Gould, J. Verreaux, G. Hartlaub,

P. L. Sclater, R. B. Sharpe, E. Oustalet, H. E. Dresser, J. Cabanis, T. Salvadori and A. Reichenow.

These ornithologists increased greatly our knowledge of the regional diversity of the avifaunas of the world but none of them seems to have seriously pondered the problem of distinguishing "real species from local varieties", i.e. distinguishing "between those characters which were impressed on a species at its creation, and those which may be reasonably attributed to external agents", a problem which Strickland (1845: 219) clearly posited in his well-known report on the state of ornithology. Geographical population differences had been mentioned in the literature since the time of Linnaeus, Buffon, Kant, Zimmermann, Esper, Pallas, and even earlier, during the 18th century (Mayr 1963, 1982, Zirnstein 1981).

Throughout most of his life, John Gould (1804–1881) considered any sample of birds that differed morphologically as a morphospecies. However, his work on Darwin's bird collection from South America and the Galapagos Archipelago proved decisive, because it permitted Darwin to appreciate the importance of the phenomenon of geographic representation, one of the reasons for his accepting the theory of geographic speciation in early 1837 (Sulloway 1982a); e.g. that closely related species of *Rhea* and of *Mimus* replace each other on the mainland of South America and that most of the Galapagos landbirds, including the several forms of *Mimus*, were new species which are clearly allied to related forms on the South American mainland. Another crucial insight at that time was Darwin's realization that one could call several populations on different islands in the Galapagos Archipelago either varieties or species (Mayr 1982: 409). Gould also concluded correctly that "the Galapagos finches were not, as Darwin had previously thought, members of widely different genera or even families, but rather one peculiar group of thirteen species" (Sulloway 1982b: 21). Gould placed them in one genus and 3 closely allied subgenera. In later years, Gould occasionally commented on geographical colour differences in birds of the same species, e.g. "the Tits of Central Europe being far brighter in colour than British specimens" and "the like difference exists between specimens of the same species inhabiting Van Diemen's Land and the continent of Australia" owing to the greater density and cloudiness of the atmosphere in islands, he thought (Gould 1855).

Among the ornithologists of the late 19th century mentioned above, Cabanis, Reichenow, Sclater, Sharpe and Gadow did not deny the existence of subspecies or certain climatic varieties in nature. Sharpe and Gadow listed some of them in the volumes of the *Catalogue of Birds in the British Museum* which they prepared, designating these forms as "subspecies, α, β, γ" etc. (Sharpe 1874, Gadow 1883, 1884). However, they and a few other authors in the 'Catalogue' series (e.g. Hargitt in vol. 18) assigned binomial names to these subspecies as C. L. Brehm (1823, 1831) had done decades earlier, as well as E. Blyth (1850) and T. C. Jerdon (1862). The latter 2 ornithologists recognized conspicuous geographic variation in many species during the course of their extensive comparative studies of Palaearctic and Indian birds, yet preferred in practice to give each race a distinct specific name. Edward Blyth had corresponded with

Darwin during the 1850s. His discussion of the common descent of certain bird 'species', however, refers to geographical subspecies (which Blyth named binomially) and therefore does not mean that he implied transmutation of biological species. Jerdon (1862: xxxiii) pronounced: "That the species were created at hap-hazard, without any reference to others, either of the same group, or more distant ones, is a doctrine so opposed to all affinities and analogies observed throughout the animal world, that the mind refuses to accept it, and intuitively acknowledges the evidence of design". The use of the term "affinity" by Jerdon is in the sense of Strickland and is synonymous with "homology", but not in the sense of affinity as we would use this term today.

Many other museum ornithologists of the late 19th century very probably had accepted the theory of evolution, although this is not reflected in their taxonomic treatment of species and they never published their views on this or any related topic except, e.g., Reichenow (1893), Sclater (1896: 314) and also Alfred Newton, the doyen of British ornithologists at that time. He had been one of the first biologists to adopt the Darwinian theory of natural selection on the basis of the Darwin-Wallace articles presented to the Linnaean Society on 1 July and published on 20 August 1858 (Gage & Stearn 1988). Newton immediately applied natural selection to the interpretation of a phenomenon in nature, i.e. the origin of desert coloration in several species of larks and chats of northern Africa, and discussed his interpretation in a long letter written on 24 August 1858 to H. B. Tristram, who directly accepted this view. He presented it, with only a general reference to Newton, in an article which appeared in 1859 several months prior to the publication of Darwin's 'Origin' (Tristram 1859: 429–433, Cohen 1985: 590). Thus Tristram (and not Newton) became "the one naturalist publicly to accept and to apply the new concept of natural selection before the publication of the Origin" (Cohen 1985: 592; see also Newton 1896: 79 and Burkhardt 1982: 42). Most ornithologists at that time and into the 20th century preferred a Lamarckian interpretation of such phenomena. On the other hand, Newton never gave a clear definition of what he thought a 'species' was, although it is obvious from the context of several discussions that he followed a morphological species notion. He did not include entries for 'species' or 'subspecies' in his well-known "A Dictionary of Birds" (1896), stating in the introduction (p. viii) "Nomenclature . . . owing to its contentious nature I have studied to avoid." Newton (1896: 343) agreed with the North American ornithologists' abolition of a great number of what had hitherto passed as distinct 'species', and their recognition as local forms, any 2 or more of which should be united under one heading. During his later years, P. L. Sclater (1896: 314–315) shared a similar opinion "on the vexed subjects of trinomials" stating that subspecies should be designated with a third name following the principles of the North American students of geographical variation of birds and mammals. As examples he listed the trinomial names of several British and continental forms of tits.

Many ornithologists of the late 19th century followed A. R. Wallace's (1858) advice: "You must consider every group of individuals presenting permanent characters, however slight, to constitute a species". In discussing the question "What is a species?", David O. Hume (1875) in India similarly concluded that species differ in essential (i.e. constant) characters, however small, and not bridged over by intermediate links. Under this concept, all morphologically differentiated allopatric varieties, e.g. those inhabiting islands, were raised to the rank of separate species.

Among North American zoologists applying a narrow morphospecies concept towards the end of the last century, was C. H. Merriam (1897: 755): "... forms which differ only slightly should rank as subspecies even if known not to intergrade, while forms which differ in definite, constant and easily recognized characters should rank as species even if known to intergrade". He described no less than 78 "species" of North American bears (see Hall 1981, vol. 2: 952–958) and numerous "species" of prairie wolves (coyotes). This led to an interesting discussion on the species question in *Science* (n.s. 5, 1897), initiated by no other person than Theodore Roosevelt, who disagreed from a field naturalist's point of view with Merriam's taxonomic "oversplitting".

Explorer-naturalists: wide species limits

Ornithological exploration of the vast and ecologically diverse continents of Eurasia and North America during the 18th and 19th centuries led to the discovery of numerous conspicuously different, but intergrading geographical forms of birds and mammals which the explorer-naturalists combined in rather broadly circumscribed species taxa. The European explorers were most active during the first half of the 19th century, their principal reports appearing in 1811, 1833, and 1840–1867. Most of them worked under the influence of the typological theories of natural philosophy, whereas in North America systematic ornithological exploration began somewhat later reaching a peak during the 1870s and 1880s after the publication of Charles Darwin's theories of evolution. The European explorer-naturalists studied their collections of birds and mammals at different museums and some of them became museum specialists. Most of the North American naturalists mentioned below were associated with the Smithsonian Institution in Washington or with the American Museum of Natural History in New York.

Old World: the Gloger-Middendorff school.

The founder of this research tradition was P. S. Pallas, who travelled in Siberia and the Far East (1768-1774). He was followed by F. Faber (Iceland 1819–1821), J. H. Blasius (Carpathian Mountains 1835, Russia 1840–1841), A. von Nordmann (southern Russia 1837), A. Th. von Middendorff (Lapland 1840, Siberia and Far East 1842–1845), L. von Schrenck (Far East 1854–1856), and G. Radde (eastern Siberia 1855–1859, southern Russia 1860s–1890s). Several of these men travelled under the auspices of the Academy of Sciences in Petersburg to explore territories of the vast Russian empire. Other early explorer-naturalists in the services of the Academy of Sciences in Petersburg who had travelled in eastern Europe and Asia during the 18th century were D. G. Messerschmidt, G. Steller, S. G. Gmelin, and J. A. Güldenstädt. The results of the researches of these latter workers have been utilized and in part published by P. S. Pallas. Constantin Gloger (1833, 1834, 1856a,b) and Hermann Schlegel (1844a,b), museum workers in Berlin and Leiden respectively, and naturalist travellers in Europe became influential among the above group of explorer-naturalists through their theoretical reflections on the nature of species and their discussions of general aspects of individual and geographic variation.

Peter Simon Pallas laid the foundations of zoological, geological, and geographical knowledge of vast portions of the Eurasian continent. He distinguished in his important 'Zoographia Rosso-Asiatica' (1811) between individual and geographical variation and found that numerous wideranging species consist of a mosaic of morphologically characterized climatic varieties (Stresemann 1962). His statement "Varietates nullas neglexi, quae in Zoologia maximi momenti certae sunt" influenced the work of those who succeeded him in the faunal exploration of Eurasia and led to their preliminary studies of the significance and cause of geographical variation. However, based on the strongly typological view of nature which soon developed under the influence of German idealism and Naturphilosophie, Gloger, Schlegel and Blasius (as nearly all other European naturalists at that time) conceived species as immutable natural entities which had independent origins and varied geographically within definite limits (due to climatic or other environmental influences). Schlegel in Leiden (Netherlands) eventually became convinced, like C. L. Brehm and the entomologist H. Schaum in Germany, as well as L. Agassiz in North America, that also all geographical varieties had existed since the beginning of creation and were immutable (Stresemann 1975: 200).

In his study of the birds of the far northern regions, Faber (1825) developed the view, confirming Pallas's, that many widespread species have changed their appearance due to the influence of the local environment (climatic races). C. L. Gloger's (1833: x) species definition was "What under natural conditions regularly pairs, always belongs to one species." He prepared the first comprehensive treatment of general aspects of the "Variation of birds under climatic influence" (1833), in particular with regard to plumage colour. This small book (159 pages) was originally prepared as the Introduction to Gloger's (1834) "Handbook" of the natural history of European birds when Gloger was in his twenties and still a student of natural sciences in Berlin (where he used the extensive bird collections) under H. C. Lichtenstein. The text was issued separately to come to the attention of a wider circle of naturalists outside the narrow field of ornithology. Stimulated by the observations of P. S. Pallas (the "excellent, well informed, true naturalist"), Gloger emphasized the regional intergradation of climatic varieties of birds which should not be separated artificially as "species". His theoretical species concept was typological and his taxonomic species category widely delimited. Gloger's observations on continuous gentle character gradients "which connect even the most distant extremes", anticipate the phenomenon of clinal character variation in current terminology. He also mentioned geographic variation of northwardly increasing body size, geographical differences of egg coloration, calls and song and even of behaviour and habitat preferences. Gloger (1833: 106–107) thought, however, that the character variation of geographical races is caused by direct influences of the climate and that the offspring of individuals of one variety, if transferred to the range of another one, would change to that plumage colour within a few years. He therefore proposed that climatic varieties not be named and existing names be placed under the synonymy of the species name, a suggestion which practically no later naturalist has followed.

Gloger (1833, 1834) concluded on the basis of intergradation as demonstrated by intermediate specimens that, e.g., *Sitta caesia* is conspecific with *S. europaea, Corvus cornix* with *C. corone, Motacilla lugens* and *M. lugubris* with *M. alba, Garrulus bispecularis* with *G. glandarius*. Many of Gloger's species coincide with current polytypic biospecies. In certain other cases, however, Gloger's 'lumping' tendency led him to combine as 'varieties' the vicariant members of species pairs, since he had no information on their relationship along the contact zones: *Hippolais icterina/H. polyglotta, Emberiza caesia/E. hortulana, Sturnus unicolor/S. vulgaris, Phoenicurus erythrogaster/P. phoenicurus* and *Parus monticolus/P. major*. In the words of a leading contemporary ornithologist, Gloger's accomplishments "have been epoch-making and, even though questioned in part by recent research, and partly recognized as erroneous, have been highly stimulating in his time" (Hartlaub 1865: 1). Gloger's pioneering contributions were little appreciated during the late 19th and early 20th centuries until Rensch (1929b) and Mayr (1942, 1982) made reference to his work repeatedly.

The taxonomic philosophies of Pallas, Gloger and Schlegel were followed by the naturalists-explorers in their ornithological expedition reports: Nordmann (1840), Blasius (1844), Middendorff (1853, 1867, 1874), Schrenck (1859, 1860) and Radde (1862, 1863, 1884), all of whom compared their material with samples from western and eastern Europe. Only Nordmann, however, accepted Gloger's suggestion not to differentiate the geographical varieties by name. The other explorer-naturalists beginning with Middendorff followed Schlegel (1844a,b, 1854–58), who had, as the first zoologist, consistently applied trinomial nomenclature to a fairly large number of geographical varieties (his "conspecies"), the name of the conspecies following the species name directly, e. g. *Falco tinnunculus japonicus*. When he worked on the material which Ph. F. Siebold had collected in Japan, Schlegel (1844b) simply added the geographically descriptive term *japonicus* to the species name to characterize the morphologically deviating Japanese island population. He followed the same method (1844a) listing 22 geographical conspecies of European birds. Middendorff, Blasius and the other naturalists, however, inserted the expression 'var.' (*varietas*) between the species and subspecies name, as Sundevall (1840) had done in several cases before.

The ornithologists of the Gloger-Middendorff school used the term variety mostly, if not exclusively, in the sense of geographical subspecies. Other contemporary workers did not always distinguish individual from geographical varieties. Therefore, the use of the term variety was eventually abandoned (Mayr 1963, 1982).

Middendorff (1853) and the other naturalists had at their disposal many series of specimen samples representing numerous taxa from far distant regions of Eurasia. This material demonstrated various aspects of individual and geographic variation including the direct intergradation of many contiguous taxa of birds and mammals (bears, foxes, wolves, hares) in colour, measurements and form, thus revealing the conspecific nature of numerous narrowly conceived morphospecies of previous authors, e.g. the conspicuously different subspecies of such wide-ranging bird species as *Garrulus glandarius, Motacilla alba, Pyrrhula pyrrhula, Sturnus vulgaris* and *Eremophila alpestris*. Turning against one of his ornithological critics, Middendorff (1874: 1230) stated: "Nature appears very different to the travelling naturalist when he daily pursues his researches amidst the richest animal life, impressed by its endless shapes; and very different to the specialist handling a few dry skins in a museum." In a chapter entitled "Umfang des Artbegriffes" [Extent of the species notion], Middendorff (1867: 790–798) stated his basic agreement with Gloger's broad taxonomic species category but emphasized that he doubted in many cases the external cause of geographic variation to lie in climatic influences. He dismissed Darwin's transmutation theory because by far the majority of the (broadly delimited) species appeared to him sharply separated by bridgeless gaps. He favoured a typological species notion and stated that transmutation may apply to only few species taxa.

Nordmann (1840), Schrenck (1860) and Radde (1863, 1884) discussed similar taxonomic observations on the species which they had collected during their expeditions, so that several contemporary reviewers of their expedition reports spoke of the "Gloger school" (Homeyer 1868) or the "Middendorff school" (Hensel 1861). It is obvious from the publications of the members of these 'schools' that they considered themselves to be part of a research tradition. They referred frequently to the general discussions of Gloger and Middendorff. Radde (1884: 11) quoted the concepts of P. S. Pallas as the theoretical basis of his work. These explorer-naturalists realized at the same time that most contemporary ornithologists in Europe opposed their application of wide species limits (i.e. their broadly defined taxonomic species category). There were only few other taxonomists in Europe who followed Schlegel (1844a) in using, at least in some cases, trinomials for subspecies; e.g. Zander (1851) considered the various conspicuously different geographical forms of *Motacilla alba* and *M. flava* as conspecific and Wied (1858: 27, 101) listed trinomial names for 2 North American birds (*Otus brachyotus americanus* and *Hirundo riparia americana*).

Besides many taxonomic aspects of their collections, the ornithologists of the Gloger-Middendorff school also studied numerous general phenomena of geographical character variation of birds and mammals across Eurasia, especially the variation of body size and of the colour of plumage and pelage, respectively. In a lengthy chapter on 'The variation of Siberian animals', Middendorff (1867: 798–822) continued the tradition of Gloger (1833) and treated continental variation of vertebrates comprehensively emphasizing that body size of members of the same animal species increases from Africa through Europe to northeastern Asia (without, however, referring to Bergmann's earlier publication on this topic; regarding the history of Bergmann's Rule see Coleman 1979). Middendorff pointed out that a colourful and shiny plumage characterizes tropical birds, but not exclusively, as shown by the shiny portions of the plumage in such northern birds as *Luscinia suecica, L. calliope* and

Somateria spectabilis. He further stated that, under the cold continental climate of northeastern Siberia, plumage colour turns increasingly whitish in many bird species and, on the other hand, becomes gradually more intensive and darker under the humid oceanic climate of the coastal lowlands both east and west of the Bering Sea, extending into humid Amurland, where Schrenck (1860) had made similar observations. The latter explorer had stressed the fact that plumage colour in birds of the Amur region darkens through an increase in the black, grey, blackish brown and grey-brown pigmentation, with or without an extension of the dark portions of the plumage patterns.

The naturalists of the Middendorff school were too weak as a research group to constitute strong opposition to the leading, systematic ornithologists of their times (who applied narrow taxonomic species categories). The members of the Gloger-Middendorff school remained 'outsiders' during the 19th century. Moreover, since they published the results of their ornithological studies only in costly expedition reports which had limited distributions, their consistent emphasis on broadly defined species entities of Eurasian birds and mammals, together with their impressive data base on geographical variation, had not the impact among fellow workers of the scientific community as would have been desirable. Probably for the same reason, the research tradition of the Gloger-Middendorff school existing during the course of over 100 years (1770s to 1880s and beyond) has not been widely appreciated previously by ornithological historians, although the significance of the early work of P. S. Pallas has always been stressed.

Hermann Schlegel at Leiden and J. H. Blasius at Brunswick made great efforts to assemble, from the 1850s to the 1870s, series of specimens representing young and adult birds of the various geographical 'conspecies' in order to determine the range of individual and geographical variation of a species and to analyse regional trends in the variation of plumage colour and body size (Baldamus 1861, F. Schlegel 1867). They adhered to a similar typological species concept as Gloger (1833) and Middendorff (1853) but assigned species taxa to a somewhat less broadly defined taxonomic species category. In their lists of the birds of Europe, both Blasius (1862) and Dubois (1871) used subspecies names routinely, as Schlegel (1844a,b) had done. However, Blasius and Dubois designated the subspecies of a species with the letters α, β, γ, etc. They did not go as far as Gloger (and later Kleinschmidt) in 'lumping' certain geographical representatives into the same species; thus they circumscribed species at an intermediate level of microtaxonomic differentiation (Table 2). The list by Blasius (1862) was "privately printed" in Germany and an English translation issued by A. Newton. The catalogue by Dubois resembles that of Blasius but follows a different sequence. Both publications are scarce and little known. Dubois (1873) later discussed geographical variation in many birds, adding several subspecies to his previous list and deploring the application of narrow species limits by many leading systematists in Europe.

J. H. Blasius was not an evolutionist. He stated that a bridgeless gap separates 2 different species, "a sharply defined boundary, free from all gradual transitions must occur". If the characters of geographical forms intergrade, specific separation is not justified. Environmental factors may cause certain geographical deviations from the type; they cannot, however, destroy the integrity of the species. All species represent independent creations. An unshakeable order rules organic nature, as it also rules the worlds of crystals and stars (Blasius 1857: v, 1858, 1861). Most leading ornithologists in Germany at that time supported this typological and creationist, non-evolutionary viewpoint.

Only a few ornithologists had adopted Darwinian interpretations (e.g. F. Kutter, G. Jaeger, W. von Reichenau; see Stresemann 1975). Among the latter were also Anton Reichenow in Berlin and Hans Baron (later Count) von Berlepsch in Hannoversch-Münden. Reichenow had travelled in Central Africa during 1872/73. According to his Darwinian view "all extant animal species basically are varieties of older extinct forms" and the study of geographical variation was furnishing with inestimable material those naturalists who based their systematic studies upon the theory of evolution. At that time, Reichenow subordinated the geographical subspecies under the species category and delimited fairly wide species taxa, describing numerous geographical forms from Africa (Reichenow 1877, 1880). Since the early 1880s, Berlepsch applied trinomial nomenclature in his studies of neotropical birds, probably influenced by the practice of Coues, Allen, Ridgway and other North American ornithologists some of whom also worked on Neotropical birds. Berlepsch distinguished 16, 17 and 19 trinomially named subspecies among 216, 177 and 289 forms, respectively, in 3 separate publications on birds from western South America (e.g. Berlepsch & Taczanowski 1883). Stimulated by the discussion of trinomial nomenclature at the British Museum during the visit of E. Coues in 1884 (Sharpe 1884, see below) and at the suggestion of G. Hartlaub, the German Ornithological Society, during the same year, discussed and agreed on the modest use of subspecies names. Based on this official licence, several European ornithologists continued or began to apply trinomial subspecies names to a modest degree (besides Reichenow, Berlepsch, Taczanowski and Seebolm, also several Russian workers like Sewerzow, Bogdanow and Menzbier). L. Taczanowski in Warsaw had listed mostly narrow morphospecies in his work on Southern American birds during the 1880s but, in his summarizing treatment of the bird fauna of eastern Siberia, he discussed numerous trinomially named subspecies (Taczanowski 1891–1893). Berlepsch was an evolutionist (like Reichenow) and, during the early 1890s, he lectured on the genealogical relationships of certain groups of birds and on various aspects of Darwin's theory of natural selection. (Regarding Berlepsch's and Reichenow's later opinions on a peculiar use of trinomial nomenclature, see below.)

The contrasting views of most museum ornithologists in Europe and of the explorer-naturalists of the Middendorff group regarding narrowly and broadly defined taxonomic species categories, respectively, led to numerous controversies, particularly in Germany. Between 1826 and 1832 (in Oken's *Isis*), Faber, Gloger and Bruch repeatedly attacked C. L. Brehm's concept of a narrow taxonomic species category and his use of 'subspecies' discussing various aspects of individual as against geographical variation which Brehm had not clearly separated. This controversy lingered on in the literature until the German Ornithological Society (DOG) devoted its annual meeting in 1856 to an extensive discussion of the question "What is a species?" without solving the problem or reaching an agreement on the circumscription of species taxa. Temporary arguments flared up again after Darwin's publication of the 'Origin' (Stresemann 1975), but the museum specialists' view on a narrowly defined morphospecies category continued to dominate systematic ornithology in Europe and the work of the Gloger-Middendorff school fell into oblivion (hastened by an extensive unfriendly discussion of the ornithological work of Middendorff, Schrenck and Radde by a museum worker from the point of view of the narrow morphospecies concept—Homeyer 1868–1870). As mentioned above, few Old World ornithologists used subspecies names during the 1870s and 1880s until the turn of the century when, at the annual DOG meeting at Dresden in 1897, Hartert, Kleinschmidt, Berlepsch, A. B. Meyer and Wiglesworth again discussed the problem of subspecies and species, this time inspired by the work of the North American ornithologists.

New World: the Bairdian school

During the 1860s and 1870s, the leading ornithologists in North America, S. F. Baird, E. Coues, J. A. Allen and R. Ridgway, further developed the subspecies concept, after J. Cassin and S. F. Baird had named several geographical varieties of a number of species during the 1850s (Stresemann 1975, Mayr 1982, Sterling 1988). These workers began to apply trinomial nomenclature to a modest degree when Baird, Cassin & Lawrence (1860) listed some 'varieties' of *Picus villosus, Mniotilta varia, Tringa alpina* and *Bubo virginianus*, those of the latter species even without the usual expression 'var.' in front of the subspecific name. Their use of trinomial names increased conspicuously during the 1870s (Coues 1872, 1874, Baird, Brewer & Ridgway 1874) and during the 1880s, e.g. Ridgway (1881), who left off the expression 'var.' in front of the subspecies name routinely (as had Schlegel 1844a,b in Leiden) and Baird, Brewer & Ridgway (1884). In 1885, certain rules on the use of subspecies names were adopted unanimously by the American Ornithologists' Union and the slogan "Intergradation is the touchstone of trinomialism" (Stejneger 1884) became the guiding principle in North America (A.O.U. Code 1886, review by Allen 1890, 1908). Cutright & Brodhead (1981) summarized these developments, emphasizing the role of Elliott Coues, who was probably most responsible for the spread of trinomial nomenclature in North America.

In contrast to the typological and non-evolutionary (pre-Darwinian) concepts of most European workers, the theoretical views of this new generation of North American ornithologists were fully in accord with the theory of evolution (though regarding the mechanism of evolutionary change they preferred a Lamarckian interpretation—Allen 1871, Elliot 1892). Thus Coues (in Baird *et al.* 1874: 559), in a somewhat oversimplified manner, defined the geographical variety as "a nascent species". The North American ornithologists defined species morphologically like Wallace (1858), Hume (1875) and others had done (see above) stating that "a small amount of difference, if constant, was considered 'specific', in a proper sense, while a large amount of difference, if found to lessen and disappear when specimens from contiguous faunal areas were compared, was considered as not specific" (A.O.U. Code 1886, cited from Allen 1908: 594). Many allopatric forms were raised to the rank of separate species, whereas others were considered as conspecific based on overlapping individual variation or simply on personal judgment (Ridgway 1901: x).

The American ornithologists were working under the direction of S. F. Baird of the Smithsonian Institution (Washington), the leading vertebrate zoologist of mid-19th century America and a very able scientific administrator. Coues (1903) later designated this period the 'Bairdian Epoch' of North American ornithology.

The ornithologists of the Bairdian school had arrived at the grouping of intergrading subspecies into widely circumscribed species taxa through their analyses of extensive specimen material (series of adult and young birds of the same species from many different locations of a species' range), which they had collected as physicians and naturalists of several transcontinental military expeditions organized by the Geological Survey in Washington to explore locations for railroad routes in western North America. These expeditions were run in an east-west direction at intervals northwards between the Mexican and Canadian borders and the collections sent to the National Museum at the Smithsonian Institution. The analyses of these collections resulted in important contributions to the study and interpretation of individual and geographic variation of birds in body size and relative size of extremities, of size and shape of bill and wings, and on plumage colour, including the repeated emphasis on the gradual, i.e. clinal, nature of geographical character variation (Baird 1866, Allen 1871, 1875, 1876, 1877, Coues 1871, 1872, 1873, Ridgway 1872, 1873). In discussing certain aspects of plumage colour variation, Ridgway (1873: 549) referred in detail to some of the results of Gloger's (1833) early work.

W. Bock (pers. comm.) pointed out that the reason for the change in the thinking of North American ornithologists on the species concept probably developed from the very nature of the massive surveys of the American West, beginning with the early railroad surveys. These surveys were basically practical in nature, the goal being to investigate the potential of the vast areas of the west in order to make decisions on future uses of the land, e.g. for farming, grazing, etc, and hence the need to collect numerous geographical samples of animals and plants, as well as to collect large samples from each locality. These large collections of series of individuals of each species from numerous geographic localities established the foundation for the concept of geographic variation and of the subspecies concept, which had its major development among the North American ornithologists during the second half of the 19th century. Whereas topography, climate and animal populations change fairly gradually over large distances in Eurasia, animals and plants in the American West with its diverse terrain and climate are subdivided into numerous local forms, often with reasonably strong differences between the local populations. Hence the very nature of the material available to the American ornithologists for study permitted them to develop the subspecies concept quite easily.

There are interesting historical similarities between the coinciding taxonomic interpretations and the comparable application of fairly broad limits of morphospecies by the American ornithologists and by the earlier exploring ornithologists in Europe, arrived at independently by these 2 groups, although the researchers in North America were, of course, aware of many European publications. For example, several European articles and books are referred to in the 'Introductory Remarks' of Baird *et al.* (1860); the same was the case in the opposite sense, e.g. papers by S. F. Baird in 1866 and by Ridgway in 1879 were reissued in German during the same year of publication in the *Journal für Ornithologie*, where major ornithological books and articles were regularly and extensively reviewed; the same applies to *Ibis* in Britain. However, I did not find any evidence that the expedition reports of Nordmann, Middendorff, Schrenck and Radde were known in North America. The explanation for these similarities would seem to lie in the fact that both groups of ornithologists worked with ample specimen material (more extensive in the case of the North American workers) collected over large continental regions. Their analyses revealed several significant aspects of both individual and gradual geographical variation of bird species, and Rensch (1929b) later named after them certain regularities which they had discovered regarding the geographical variation of plumage colour and relative length of extremities (Gloger's and Allen's Rule, respectively). Although the North Americans were evolutionists considering species to be related to one another genealogically and the Europeans were creationists assuming an independent origin of each species, their taxonomic procedures were virtually identical; in other words, both groups were working under different theoretical species concepts but had developed comparable and broadly defined taxonomic species categories.

Like Gloger (1833) 40 years earlier, Allen (1871) also on the basis of his Lamarckian interpretation of geographical variation, suggested not recognizing subspecies names; but, as in Gloger's case, this proposal was not accepted by other ornithologists and Allen himself soon abandoned it, employing subspecies names routinely in subsequent years. In view of the discussion which soon developed in America and in Europe regarding the 'oversplitting' of species which vary gradually (clinally) over large regions (beginning with Allen 1890), it is surprising that no other method than the formal description of subspecies was proposed for the analysis of geographic variation of birds until several decades later (e.g. graphical mapping with the help of contour lines). The reason probably is that the 19th century ornithologists who employed trinomial nomenclature often treated 'subspecies' quite typologically, almost like a morphological species at a lower categorical rank (Mayr 1982: 289). The attitude of their minds was still conditioned to a taxonomy of discrete units and variation, and their nomenclature was based on it. However, the collecting of large numbers of specimens and their study in 'series' ('suites'), beginning in ornithology with the naturalists of the Gloger-Middendorff school and H. Schlegel in Europe and, in particular, with Agassiz (fishes), Baird, Coues, Allen, Ridgway and other ornithologists in North America, eventually led to the overcoming of the prevailing typological view of variation and the development of 'population thinking', which was "perhaps the greatest conceptual revolution that has taken place in biology" (Mayr 1963: 5).

The mission of Elliott Coues to London in July 1884 to propagate the application of wider species limits and the use of trinomials by European ornithologists failed completely. The opposition of zoologists at the British Museum was too strong (Sharpe 1884). Only Henry Seebohm, who was among Coues' audience, agreed with him. Seebohm had been influenced by Darwin's theories of evolution and by the work of the North American ornithologists. During his travels in Europe and Siberia, Seebohm had studied the intergradation of many so-called 'species' such as, e.g., *Sitta caesia/S. europaea* and *Corvus corone/C. cornix* (Seebohm 1882–1883: xi, 547, 1901: 500–504). In those years, only a few European ornithologists besides Seebohm (1882–1883, 1882) and Radde (1884) opposed the application of narrow species limits (e.g. Severzow 1873, Reichenow 1877, Berlepsch & Taczanowski 1883) until Victor von Tschusi (1890) in Austria also began to combine subspecies into wide morphospecies taxa following the principles of the North American workers, i.e. applying a truly trinomial nomenclature. On the other hand, a few European workers continued to designate subspecies with the old-fashioned expression 'var.' even into the present century (Dubois 1909, 1912). Tschusi (1890) believed that certain species characters are constant and others like colouration and colour pattern vary within rigid limits which variation cannot transgress. As discussed below, Seebohm's theoretical ideas were later to influence the development of the biological species concept in Europe when E. Hartert and O. Kleinschmidt entered the discussion during the 1890s.

The pre-Darwinian species concept of Otto Kleinschmidt (1870–1954)

In the tradition of the Gloger-Middendorff school as well as the work of H. Schlegel (1844a,b) and J. H. Blasius (1862) decades earlier (and long since largely forgotten*), Otto Kleinschmidt (1900, 1926) again emphasized a strongly typological-creationist theoretical species concept and formulated a broadly defined taxonomic species category. He thus delimited species taxa widely, combining weakly to strongly differentiated geographical forms in one unit, a "natural species" which he called "Formenkreis" (array of forms). His intention was to distinguish this assemblage from the monotypic Linnaean species of many contemporary museum ornithologists in Europe and to facilitate the application of this method also by those workers who did not want to abandon the narrow meaning of the term 'species' (Mayr 1942: 112). The component forms of a Formenkreis represent and more or less exclude one another geographically. Kleinschmidt gave each of his Formenkreise a new capitalized

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*Although Kleinschmidt and several other ornithologists did mention incidentally some papers of these early workers, the relevance of the latters' arguments regarding a broadly defined taxonomic species category apparently was appreciated by only a few ornithologists (e.g. Hartert 1901: 216) in the discussions of microtaxonomic concepts around the turn of the century (see also below).

group name, e.g. *Parus Meridionalis* for the Marsh Tit (*P. palustris*) and *P. Salicarius* for the Willow Tit (*P. montanus*), to emphasize the difference between taxa of this broadly defined new taxonomic category and the taxa of the narrowly defined Linnaean species category. This procedure, although logical, is not acceptable under the rules of nomenclature and was followed by practically no other systematist.

At the beginning of this century, Kleinschmidt's efforts, together with those of Ernst Hartert (see below), led to the replacement of the morphological species concept by the biological species concept in Europe, although Kleinschmidt's own theoretical views were basically pre-Darwinian and typological in nature. I emphasize, however, that most of the Formenkreise which he discussed in his monograph series 'Berajah' represent valid taxa (mostly species and superspecies) and many details of Kleinschmidt's methodology, such as his meticulous character analyses and his views on the importance of geographic representation, were highly influential during the first decades of this century (Stresemann 1936: 155, Mayr 1942: 112).

Like the workers of the Gloger-Middendorff school and the ornithologists in North America (e.g. Allen 1871: 186–250), Kleinschmidt documented important data on the individual and geographic variation of Palaearctic birds. His rediscovery of the specific distinctness of 2 sibling species of grey tits (*Parus montanus* and *P. palustris*) led him to emphasize repeatedly what Lamarck in 1786 had stated in these words: "Two species constantly distinct in reproduction sometimes offer less differences between them than do two varieties of the same species" (Burkhardt 1987: 163); similarly Darwin: "Hence species may be good ones and differ scarcely in any external character" (Notebook B: 213 cited in Mayr 1982: 266); and also Gloger (1856a,b: 283, 301). In discussing Kleinschmidt's concept of the Formenkreis, Hartert (1901: 216) compared it to the species notion of C. L. Gloger, J. H. Blasius and G. Radde. In a similar manner, Stresemann (1936: 154) emphasized that "There is not the slightest difference between his 'formenkreis' and the 'species' of Gloger and other Pre-Darwinists". Comparable to the views of these earlier workers, Kleinschmidt's theoretical species concept was typological-creationist and his taxonomic species category (Formenkreis) was broadly defined.

The typological nature of Kleinschmidt's theoretical viewpoint has been clearly recognized and specifically emphasized by several authors of the anti-Darwinian philosophical literature (Conrad-Martius 1938: 250ff, 1949, 1952) and of the creationist literature (Illies 1983: 118). The basic theoretical attitude of Otto Kleinschmidt (1870–1954) was probably determined by his religious commitments as a protestant pastor, his own claims to the contrary notwithstanding. Eck (1990: 62) stated similarly that Kleinschmidt's theoretical views (with roots outside the natural sciences) may have been influenced by his theological convictions. Under the guidance of his deeply religious mother and of several protestant teachers, he had decided to become a pastor when he was in his teens. His systematic work on birds (beginning in 1892 when he was a student of theology) was done against the background of a deeply religious world view. Kleinschmidt (1900) formulated his broadly conceived taxonomic species category of the Formenkreis after studying, during the 1890s, several geographically variable species (e.g. *Garrulus glandarius*), various sibling species ("parallel species", as he called them) in the genera *Parus, Certhia, Regulus* and the large falcons of the *Falco rusticolus* group. The Formenkreis as a taxonomic category was based on Kleinschmidt's typological-creationist theoretical species concept and his pre-existing religious attitude, through which he was sensitive to the theoretical implications of the specific distinctness of sibling species and the general lack of transitional forms between any of the sharply separated species that he studied. The discussions of Kleinschmidt's views by several recent biologists (Kelm 1960, Jahn *et al.* 1982: 540) seem biased due to an emphasis of certain selected ('modern') aspects of the theoretical basis of Kleinschmidt's work. For this reason, and in view of the historical importance of Kleinschmidt's interpretations, I present my analysis of his views in some detail below.

Like many pre-Darwinian systematists in Europe, Kleinschmidt (1900, 1926) taught that faunas are composed of "natural species", his Formenkreise. Each Formenkreis taxon is fairly uniform and sharply delimited like a crystal representing an independent unit from its beginning and with a separate "evolutionary" history. From his theoretical species concept he concluded that at the core of each Formenkreis (hidden behind the outside appearances of colouration and form) lies its essence (*sein Wesen*—Kleinschmit 1909: 1). Only the racial characters, not the essential characters, vary, causing the geographical differentiation of a Formenkreis (species). Individual variation of species characters resembles the regular and constant swinging of a pendulum. In Kleinschmidt's (1926: 109) words which characterize his theoretical species concept: "Each Formenkreis presumably had an independent area of origin, an independent time of origin and an independent process of formation (*Werdegang*) with an independent rate of transformation, in a word each had an independent world history (*Weltwerden*)." Kleinschmidt assumed that this is true even for very similar sibling species, e.g. Willow Tit *Parus montanus* and Marsh Tit *P. palustris* for which he stated (1921: 27): "And if the ancestors of *Parus Salicarius* and *Parus Meridionalis* once have been only two equal and microscopically small glass-clear droplets of protoplasma, they were two! (*sic*)" Even though Kleinschmidt assumed that the Formenkreise (species) underwent transformation through time and differentiated into varying numbers of geographical forms, the species had, in his view, no common history of branching evolution, each Formenkreis representing an independent "type".

Based on his superb knowledge especially of Palaearctic birds and applying the principles of his taxonomic species category of the Formenkreis, Kleinschmidt gathered related and geographically representative taxa in one Formenkreis. Due to his typological viewpoint, he placed all these taxa at the same low taxonomic level, designating them as subspecies trinomially despite their often drastically different taxonomic modification (weakly defined subspecies to vicariant species) and despite the peripheral range overlap of some representative forms, e.g. *Pluvialis apricaria*/*P. dominica, Uria lomvia*/*U. aalge, Picus major*/*P. syriacus, Luscinia* *megarhynchos/L. luscinia, Loxia pytyopsittacus/L. curvirostra/L. leucoptera, Passer domesticus/P. italiae/P. hispaniolensis*, and others. His broadly conceived taxonomic species category of the Formenkreis was, however, not precisely defined. In some Formenkreise, Kleinschmidt did distinguish between main or "capital" forms and subtle forms. In current terminology, Kleinschmidt included in one Formenkreis a monotypic species or a polytypic species, several vicariant biospecies of a superspecies or even a set of more distantly related and geographically representative species (e.g. the nutcrackers *Nucifraga caryocatactes—N. columbiana*, Hazel and Ruffed Grouse *Tetrastes bonasia—T. sewerzowi—T. umbellus* and the spruce grouse *Dendragapus falcipennis—D. canadensis*; see Eck 1970). Kleinschmidt's combining in one Formenkreis (species) even strongly differentiated and, in some cases, partially sympatric representatives (not very closely related biospecies) and still designating them trinomially as subspecies is understandable from the typological basis of his theoretical species concept, which led him to consider geographic character variation among representatives as rather superficial and comparatively minor, leaving the basic essence of a species untouched.

Although many of Kleinschmidt's Formenkreise represent polytypic biospecies and superspecies (Eck 1990), his taxonomic procedures led to strong objections by many contemporary ornithologists. Possibly to comply with some of these objections, Kleinschmidt (1940) distinguished, late in his life, more strongly differentiated "sectors" of a Formenkreis and more weakly differentiated "forms". At the same time (1941), he classified the Formenkreise into several different categories. Among German ornithological authors who followed Kleinschmidt's philosophy were, e.g., A. von Jordans, K. Meunier, H. Frieling and F. Peus.

Under his typologically conceived theoretical species concept and the broad taxonomic species category of the Formenkreis, Kleinschmidt outlined monophyletic taxa which, however, are not differentiated at the same level of the taxonomic hierarchy. Therefore, the Formenkreis is not directly comparable with any of the evolutionary taxonomic categories defined under the theoretical biospecies concept (species, superspecies, subgenus), although it comes close to, without being identical with, the "zoogeographical species" (Mayr & Short 1970) which comprises independent biospecies and superspecies. A similar composite of variously differentiated geographical representatives as the Formenkreis (occasionally with overlapping distributions of the component species) is the "*soort-complex*" (species complex) as traced among various groups of butterflies by Toxopeus (1930).

Further developments

In opposition to Kleinschmidt's and Hartert's views, the German ornithologists Count von Berlepsch (1898, 1911) and Reichenow (1901, 1911) abused, from the turn of the century, trinomial nomenclature in a very unusual manner (which was in contrast to their own previous practice since the 1870s). They applied trinomina to closely related geographical representatives, which they now, however, no longer considered as subspecies of a single species unit but as distinct, narrowly defined morphospecies ("conspecies"; not conspecies *sensu* Schlegel). They said that these separate species are similar morphologically to the binomially named species with which the "conspecies" are grouped (e.g. they can often be identified only with the help of comparative material). For this reason, Berlepsch and Reichenow objected strongly when Hartert (1897) proposed to duplicate the species name in nominate subspecies (also Lorenz 1892: 17). This taxonomic procedure, of course, demonstrated the subordination of subspecies under the species which was logical under Hartert's scheme but was impossible to accept under Berlepsch's and Reichenow's newly established notion of "conspecies".

During the first decades of this century, many North American ornithologists continued to adhere strictly to extant morphological intergradation as a necessary requirement in relating 2 geographically complementary forms as subspecies (Miller 1955). Intergradation was understood to comprise either gradual geographical blending of interconnected populations or overlapping of individual variation in geographically separated (allopatric) populations on islands or on the continent (Stone 1903, 1935, Grinnell 1918, 1921). The hybridizing woodpeckers *Colaptes auratus* and *C. cafer* continued to be considered as species, and Dwight (1918, 1925: 103) believed that species taxa possess intrinsic qualitative characters which he assumed are fundamental and constant. He further stated that these characters "underlie the other variations and determine, within specific limits, size, shape, pattern, and color." Species limits were drawn on the basis of morphological evidence and degrees of difference until Chapman (1924) suggested that each situation should be judged biologically on its own merits, thereby dismissing the exclusive application of the concept of morphological intergradation. In his extensive and meticulous work on African birds, Admiral Lynes (1926: 347) followed Chapman's principles of discriminating between species and subspecies of birds.

The broadly defined evolutionary-morphological taxonomic species category of more recent authors like Geyr (1924, 1929), Meinertzhagen (1928, 1951, 1954), and Eck (1985, 1988) leads to assemblages of phylogenetically related and vicariant forms which exhibit geographically orderly (directed) character transformation throughout the continuous or discontinuous distributional range of these assemblages. Genetic-reproductive isolation of 2 taxa in contact is not a species criterion under this view. Such broadly conceived morphological species taxa (Table 2) compare with zoogeographical species (Mayr & Short 1970). Following Kleinschmidt (1940), Eck (1985) designated sharply differentiated entities within widely delimited morphological species as "sectors".

THE ASCENT OF THE BIOLOGICAL SPECIES CONCEPT

Around the turn of the 18th and 19th centuries, several zoologists independently formulated definitions of the species which come quite close to that under the biological species concept of modern evolutionary biologists, although these early definitions were still conceived in a typological frame of mind (Mayr 1957, 1968). For example, G. Cuvier, in 1798, concluded: ". . . two wild forms which live at the same place in the same climate, without interbreeding, and always maintain their differences, have to be regarded as different species, no matter how trifling the difference might be" (Stresemann 1927, 1936). It has become known in recent years, that among those naturalists who conceived species biologically was Charles Darwin. During the late 1830s, upon the return from his expedition, he interpreted the basic taxonomic entity as biospecies (Kottler 1978, Mayr 1982: 266); but, during the 1850s, he returned to a morphological species concept. The malacologist Adolf Schmidt (1857: 6) stated that "forms which are repeatedly encountered living at the same locality without blending are to be considered as distinct species". To H. W. Bates (1862: 501), who explored the insect fauna of Amazonia, the criterion of true species was "when two or more of them are found coexisting in the same locality without intercrossing." Similarly, the entomologist Th. Eimer (1889: 16) said "species are groups of individuals which are so modified that successful interbreeding (with other such groups) is no longer possible."

Among the ornithologists of that period who fully endorsed Darwin's theories of evolution was Henry Seebohm in Britain who concluded (1882: 547): "The old definition of a species having lapsed, in consequence of the rejection of the theory of special creation, it is necessary to provide a new one. The first step toward an understanding of what constitutes a species is the admission of the existence of subspecies. Two forms which are apparently very distinct, as *Corvus corone* and *C. cornix* or *Carduelis major* and *C. caniceps*, are nevertheless found to be only subspecifically distinct—a complete series of examples from one extreme form to the other in each case being obtainable. These are produced by interbreeding." Seebohm was the first ornithologist to emphasize geographical isolation as the *sine qua non* for speciation to occur and he came close to a biological concept of species when he stated that in geographical isolation, the peculiarities of two forms may "become so far separated, that should their areas of distribution again overlap they will nevertheless not interbreed, and the two species may be considered to be completely segregated" (Seebohm 1881: x) and ". . . species are so completely differentiated . . . that they may inhabit the same area without any cross-breeding between them" (Seebohm 1887: 63). He also discussed geographical variation (as opposed to individual variation) as the basis for subspecies distinction and insisted that incipient species of birds exist in considerable numbers, as predicted by Darwin's theories of evolution. Seebohm voiced his opposition to the theoretical views of nearly all contemporary systematists in Britain with strong words suggesting, e.g., that they "be exiled to Siberia for a summer to learn to harmonise their system of nomenclature with the facts of nature" (Seebohm 1901: 503).

Many ornithologists during the 19th century tacitly applied the biological species concept in their studies of the natural history of local bird faunas without, however, discussing the theoretical basis of this concept. This was eventually done in explicit terms and with many details of its implications by two entomologists in Britain around the turn of the century, Karl Jordan (at Walter Rothschild's private museum in Tring near London) and Edward Poulton, the first zoologists to become fully aware of the biological basis for the distinctness of coexisting species (Mayr

1955, 1982). Their work was in the tradition of Darwin's and Wallace's concepts of gradual evolution and speciation through the differentiation of geographical subspecies. The results of their analyses completely contradicted the saltationist theories of speciation of the Mendelians at that time (Mayr 1980a). Jordan's ornithological colleague at Tring was Ernst Hartert who, under the influence of the work of Henry Seebohm (1882–1883, 1882, 1887) and of the ornithologists in North America, had, since the late 1880s, delimited species broadly, applying the concept of subspecies and trinomial nomenclature consistently (Hartert 1891 and several papers on tropical birds during the 1890s). Later on, Karl Jordan's influence is noticeable in Hartert's work (e.g. the subspecies definition of Hartert, 1903: vi, is basically that of Jordan in Rothschild & Jordan 1903: xlii). Hartert's contact with Kleinschmidt (Kelm 1960), in particular the latter's emphasis on geographical representation of allied forms, also was of importance. Ultimately, however, Hartert and Kleinschmidt disagreed over many issues which, I think, was mainly due to Kleinschmidt's typological viewpoint. Miriam Rothschild (1983) has written a fascinating biography of Lord Walter Rothschild, and an informative history of the Tring Zoological Museum with detailed chapters on its curators E. Hartert and K. Jordan. They were able to base their wide-ranging studies on large series of local populations of birds and insects, respectively, being the first naturalists-systematists fully to implement the biological species concept. In his *magnum opus* on the birds of the Palaearctic fauna (1903–1922), Hartert presented a list of the biological species of the avifauna of this large area judging allopatric forms on their own biological merits without feeling bound to the concept of morphological intergradation as still adhered to by many North American ornithologists. The latter agreed, however, with Hartert when he united a number of European and North American bird 'species' as conspecific, e.g. forms of *Podiceps grisegena, Branta bernicla, Melanitta fusca, Circus cyaneus, Accipiter gentilis*, and others. They disagreed, however, with Hartert's inclusion of, e.g., *Lanius ludovicianus* in *L. excubitor* and *Bombycilla cedrorum* in *B. garrulus*. On the other hand, Hartert retained species status for pairs like *Corvus c. corone* and *C. c. cornix* as well as for *Carduelis c. carduelis* and *C. c. caniceps* because, he said, these forms hybridize along only narrow zones and each form maintains its overall integrity and its morphologically distinct characters over most of its distributional range. Like most ornithologists during the late 19th century (e.g. Allen 1871, Elliot 1892), Hartert believed geographic variation is caused by direct influences of the environment, an interpretation that Heinroth (1903: 103), however, dismissed pointing out that the pattern of plumage colour is very similar in many related species which inhabit totally different climatic zones. In the case of adaptive colouration of birds of the deserts and polar regions, Heinroth assumed its origin through natural selection, as Newton (letter to Tristram dated 24 August 1858; see above). and Tristram (1859) had suggested decades earlier.

The work of the Tring scientists ushered in the end of the widespread application of the concept of narrow morphospecies in Europe. The new theoretical viewpoint and the use of trinomial nomenclature were here now seen as having originated in North America. As stated above, the work of the Gloger-Middendorff school was largely forgotten, which is not as surprising as it may seem considering the totally different, non-evolutionary, theoretical attitude of the members of that 'school'. The leading ornithologists at the large museums, e.g. Sharpe, Sclater and Reichenow, continued to resist the new trend for some years and published quite unfavourable reviews of Hartert's work (e.g. Sclater 1904). However, when Hartert, Jourdain, Ticehurst & Witherby issued 'A Handlist of British Birds' in 1912 (in which Hartert was responsible for the classification and nomenclature employed) the opposition was on the retreat. A few years later, the B.O.U. Committee preparing 'A List of British Birds' (1915) had already adopted trinomials. When the last volume of Hartert's 'Vögel der paläarktischen Fauna' was published in 1922, the application of his concepts of the taxonomic categories of species and subspecies had been generally adopted in Europe. In this intellectual struggle among European ornithologists of roughly 30 years duration, several other ornithologists had also joined forces with Hartert since the turn of the century, e.g. A. B. Meyer, L. Wiglesworth, C. E. Hellmayr, J. I. S. Whitaker and H. Schalow (Stresemann 1975). Among the latter, Meyer & Wiglesworth (1898) and Wiglesworth (1898) discussed several critical aspects of individual and geographic variation in southeast Asian birds, proposing informal designations for populations representing stages in stepped or continuous character clines (as we would say today). These authors introduced numbers and certain symbols (> and <) to designate plumage colour stages between formally named subspecies, of which the latter symbols have been applied by many later systematists.

Through the increased knowledge of geographical variation of birds, ornithologists had by then recognized that, in some species, the representative forms (subspecies) can be grouped in 2 or more subspecies groups, e.g. forms of the Hooded Crow and of the Carrion Crow within *Corvus corone* or forms of the *carduelis* subspecies-group and of the *caniceps* subspecies-group of *Carduelis carduelis*. This led to Laubmann's (1921, 1932) proposal of a rather cumbersome quadrinomial nomenclature which, although consistent with the hierarchical classification of microtaxonomic categories, did not find followers among ornithologists.

One side effect of the arguments on theoretical questions of the species concept and the taxonomic species category was that ornithologists had become overly preoccupied with subspecies taxa and had almost lost sight of the species taxa themselves in regional taxonomic surveys, which became in reality subspecies lists. This is as true for Hartert's work (1903–1922) on Palaearctic birds, where he treated monotypic species and all subspecies alike (numbering them consecutively from 1 to 2300*), as it is for the 4th edition of the A.O.U. Check-list (1931) and for Peters' 'Check-list of Birds of the World', which were also essentially lists of subspecies until Ernst Mayr assumed editorship of the Peters List with volume 9 (1960) and 'reintroduced', so to speak, the species as a unit symbolized by a binomial heading for each species taxon.

Ludwig Plate, a professor at Jena, was among those general biologists who, at the beginning of this century, defended the Darwinian theories of

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*Notice Hartert's (1922 (3): vi) correction of his numbering species and subspecies from no. 2100 onward.

evolution against a growing opposition. In 1914, he conceived the species 'physiologically', stating that a species comprises all individuals which reproduce together sexually; a common bond between them facilitates mutual recognition and sexual reproduction; species taxa are real units in nature which exist independently of man. In North America, Taverner (1919) argued, in dismissing the morphospecies concept of C. H. Merriam, "the species is a definite entity and its essential character is its genetic isolation. Absence of intergradation with other forms is the only test of the species as it exists at present. There is a barrier that isolates modern specific groups one from another . . .". In the case of allopatric forms, "the possibility of intergradation . . . must necessarily be estimated under the guidance of what evidence we have." Also for Chapman (1924) "proof of distinctness of two or more forms is their occurrence together when breeding without intergradation." He confirmed that there are many species which are more similar to each other than are many subspecies of the same species. The taxonomic rank of geographically isolated taxa is to be estimated by inference, he said.

POPULATION SYSTEMATICS

Population systematics or the 'new systematics' steadily gained influence worldwide under the leadership of Stresemann, Rensch and Mayr during the 1920s, 1930s and 1940s. The emphasis was on the biological species concept and on a fairly broadly defined multidimensional taxonomic species category. Species taxa were seen as aggregates of populations which often vary clinally. Character gradients (clines; Huxley 1938a,b, 1939)* of a species may run in different directions and a 'subspecies' may belong to more than one cline. Not even the most extreme splitting will lead to homogeneous 'sub-subspecies' of clinally varying species. Morphological, ethological, physiological, biochemical, and bioacoustic characters and their geographical variation were investigated in ever increasing detail. Phenomena studied were the population continuum, zones of secondary intergradation, and geographical isolates. The publications of Rensch (1929b, 1934) and Mayr (1942) were the first comprehensive statements of this new research tradition which was soon to unify most or all systematists worldwide, including those outside the field of ornithology, and which, from the late 1930s through the 1940s, merged with population genetics and palaeontology in the synthetic theory of evolution (Mayr & Provine 1980).

During the 1920s and 1930s, Erwin Stresemann contributed extensively to a clarification of the biological species concept and a meaningful delimitation of species taxa through his many perceptive theoretical discussions of systematic concepts, thus building an important conceptual basis during the preparatory phase of the evolutionary synthesis. Although he was an evolutionist from the beginning of his scientific career

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*As shown in previous pages, gradual geographical variation of species had already been discussed briefly by Gloger (1833) for Eurasian birds and, more extensively, by Allen (1871) and other ornithologists for North American birds as well as by Wiglesworth (1898) and Meyer & Wiglesworth (1898) for southeast Asian birds. Reinig (1938a) analyzed numerous "character progressions" in Palaearctic birds and other animals. These authors, however, usually intended to solve certain taxonomic problems rather than to study independent character clines present in species populations.

in about 1910, Stresemann was influenced at first by some of the systematic principles of Kleinschmidt, but soon built on the views of E. Hartert and L. Plate (1914). As early as 1919, Stresemann adopted a biological species concept as it became standard in evolutionary biology in later decades (Mayr 1942: 119, 1957: 17, 1980b: 96, 1982: 273): "Forms which have reached the species level have diverged physiologically to the extent that, as proven in nature, they can come together again without interbreeding . . . morphological divergence is independent of physiological divergence" (Stresemann 1919a: 64, 66). "Forms which can maintain themselves separate without interbreeding when living together under natural conditions are considered as distinct species" (Stresemann 1920: 152). In the case of allopatric taxa, their rank as subspecies or species is to be determined by inference based upon several auxiliary criteria (degree of similarities in morphology, ecology, voice, etc.; overlap of the ranges of individual variation; comparison with comparable congeneric forms which are in contact and either do or do not interbreed). For several years, however, Stresemann continued to assign species taxa to a very broadly defined taxonomic category of biospecies. In 1925 and 1926, he recognized the existence of biospecies which replace each other geographically without or only rarely hybridizing along their contact zone. This discovery of closely related and geographically representative biological species (currently called allospecies and paraspecies) led Stresemann to accept Rensch's (1928) proposal to distinguish between polytypic species (*Rassenkreis*) and superspecies (*Artenkreis*)—see Haffer (1991) for further details. In later years, Stresemann delimited species more narrowly than before (see Table 2) and investigated the ecological segregation of closely allied biospecies (Stresemann 1943). He had interpreted the origin of species through allopatric speciation already in 1913 and, during subsequent years, he investigated 'mutations' as one possible mechanism of genetic change (Stresemann 1926). Chapman (1923, 1928) held a similar view but ascribed clinal character variation to direct environmental influence.

In contrast to this latter interpretation held by a majority of ornithologists at the beginning of this century, Stresemann (1919a,b,c) applied an historical interpretation to the phenomenon of clinal geographic variation. In several conspicuous subspecies pairs of European birds (*Aegithalos caudatus, Corvus corone, Sitta europaea, Pyrrhula pyrrhula*), Stresemann postulated a postglacial contact of forms which had differentiated in geographical isolation during preceding glacial periods of the Pleistocene, leading to introgressive hybridization and to the development of the observed smooth geographical character gradients. This work was originally stimulated by Kleinschmidt's (1911) discussion of geological factors in the distribution of European birds (Udvardy 1992), as well as by the early articles of Seebohm (1882) on interbreeding between forms of crows, shrikes and goldfinches, and those of Berlepsch (1885), who had discussed the hybridization between the eastern and western subspecies of the Long-tailed Tit.

Bernhard Rensch was a student at Halle during the early 1920s, and at that time visited the nearby home of Otto Kleinschmidt (Rensch 1979), who demonstrated to him the relations of many representative forms on the basis of his large private collection of birds. At the same time, Rensch worked temporarily at the Zoological Museum in Berlin with E. Stresemann who, in 1925, saw to it that Rensch was employed by this institution (Rensch 1979: 49). Influenced by Stresemann's work on geographically representative biospecies, Rensch soon revised Kleinschmidt's terminology. In 1926, he introduced the term '*Rassenkreis*' (array of races) to replace Kleinschmidt's term '*Formenkreis*' (Rensch 1926: 254). The latter term appeared to Rensch misleading because of its prior use by zoologists to designate groups of closely related species regardless of whether they were allopatric or sympatric. Although the term Formenkreis (Kleinschmidt) and Rassenkreis (Rensch) were indeed synonymous in Rensch's (1926) first article, at the International Ornithological Congress in Copenhagen (May 1926) he in fact had mentioned that a Formenkreis may comprise one or several Rassenkreise (Rensch 1929a). In 1928, he coined the term *Artenkreis* (translated into superspecies by Mayr 1931) for a complex of 2 or more vicariant Rassenkreise (Rensch 1928, 1929). Since these latter publications, the terms Rassenkreis and Formenkreis are no longer synonyms, a fact overlooked by some authors until today. The 'Genus geographicum' and the 'geospecies' (Rensch 1931: 464) are synonyms of 'superspecies' and biospecies, respectively; neither of them corresponds to the term zoogeographical species (Mayr & Short 1970). Rensch (1929b: 14) originally restricted the use of the term 'species' to monotypic species taxa, designating polytypic species as Rassenkreise. This distinction was not accepted by other authors, because it became obvious that these designations referred to different kinds of species taxa rather than to different taxonomic categories. The terms monotypic and polytypic species were introduced by Huxley (1938, 1939) independently of J. A. Allen (1910), who had used them quite freely in his review of the 3rd edition of the 'Check-list of North American birds'.

The discovery of geographically representative forms which do not or only rarely hybridize along their zones of contact (Fig. 2) and, therefore, represent biological species (Rensch 1928, 1929), eventually led to a reversal of the excessive 'lumping' tendency among ornithologists which had reached a peak in Europe under the influence of Kleinschmidt's views: e.g. several publications by Stresemann during the early 1920s (see Haffer 1991), as well as some of Hellmayr's (*Catalogue of Birds of the Americas*—1924–1942) and Stegmann's (1934, 1935) papers on broadly circumscribed species. These authors used trinomial nomenclature for the purpose of expressing genetic relationships, also of non-intergrading representatives which, in some cases, exhibit different habitat preferences near the contact zones (see also comments by Meise 1938). The occurrence of vicariant biospecies with contiguous ranges, currently called parapatric species, demonstrated that caution must be exercised when combining as conspecific representative forms with adjoining or allopatric ranges. In a comprehensive study of the climatic rules of geographic variation and of population systematics, Rensch (1929b, 1934) showed that the concepts of polytypic species and superspecies are applicable to most groups of vertebrate and invertebrate animals worldwide. He abandoned his Lamarckian interpretation of the origin of geographical variation during

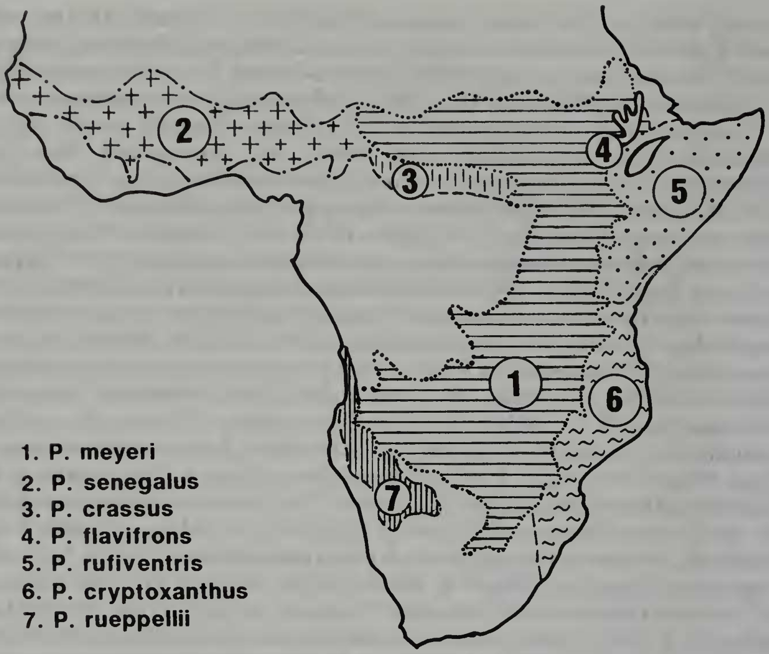

Figure 2. Distribution of the African parrots of the *Poicephalus meyeri* superspecies. Simplified after Snow (1978). This assemblage of parapatric species was used by Rensch (1928), together with other evidence, to discuss the occurrence of vicariant biospecies.

the early 1930s when be became familiar with the new redefinition of mutation as slight genetic variations which could respond to natural selection.

In North America, the systematic principles of both Hartert and Chapman regarding the ranking of taxa as subspecies and species were increasingly applied in their work by the leading ornithologists of the 1920s and 1930s, e.g. J. Chapin, R. C. Murphy, J. L. Peters, L. Griscom and many others who were also influenced by the new concepts of genetics and evolution. Chapin (1932) warned against the hasty lumping of geographic representatives under a binomial name to include groups that may have diverged to a point beyond the possibility of intergradation. He emphasized the genetic basis of slight subspecific differences knowing that "environment selects, rather than directs the variations".

Building on the work of Stresemann and of Rensch, Mayr (1942, 1963, 1970) prepared several major critical syntheses of the systematic, genetic and ecological aspects of biological species and an analysis of the speciation process. Thus he established the theoretical biological species concept in all its ramifications, based on which he defined the multidimensional species category within taxonomy. Through his contributions, the biospecies concept became one of the central tenets of the modern synthetic theory of evolution during the 1940s and 1950s, a fact too well-known to be discussed here in any detail. Lack (1944, 1949, 1971) added important data on the ecological aspects of the speciation process, as acknowledged by Mayr (1982: 274). Niche differentiation must be complete for 2 species to be able to occupy the same habitat. Therefore, several different situations may arise if species come into secondary contact (Lack 1944): (1) One species eliminates the other because it is so much better adapted ecologically, or (2) one species will exclude the other in part of its range with a narrow or broad zone of overlap developing where both are about equally well adapted; (3) the 2 forms will occupy separate but adjacent habitats in the same region of overlap; (4) both species are similar ecologically and occupy adjacent geographical regions excluding each other along the zone of contact due to ecological competition (parapatry in current terms) or (5) both species become sympatric and syntopic because they are ecologically fully isolated. Lack concluded that ecological divergence between forms must have been initiated when they were isolated from each other geographically, although it may have been intensified after they met.

In several historical essays, Mayr (1980a,b, 1988) discussed the role of systematics in the evolutionary synthesis, in particular the contributions made by naturalists-systematists (since about 1900) regarding the development of population thinking, the quantitative analysis of gradual adaptive geographic variation, and the importance of geographical speciation. Selander (1971) critically reviewed modern studies on the systematics and speciation process in birds published during the 1950s and 1960s.

In recent years, Stepanyan (1974, 1978) delimited the species of Palaearctic birds on the basis of a narrow species notion, often designating entities as species that other authors consider subspecies or megasubspecies under the biological species concept.

PHYLETIC LINEAGES AS ‘SPECIES’

Morphological-biological changes along phyletic lineages through time occur slowly (‘gently’) or more or less abruptly. However, even ‘abrupt’ shifts or changes along lineages with or without lineage splitting, are continuous and ‘gradual’, merely occurring at a higher rate than other lineages changes over time which occur at a slower rate (see Fig. 1). Shifts along lineages which may or may not be accompanied by splitting events (speciation) are taken by many palaeontologists to subdivide a given lineage into portions considered as ‘species’ in the time dimension. On the other hand, cladists subdivide lineages exclusively at splitting events regardless of whether considerable morphological-biological shifts have occurred along only one or both lineages at the time of the splitting event (Willmann 1983, 1985). Since there is no method of subdividing the evolutionary continuum of phyletic lineages in a meaningful and non-arbitrary manner, it appears best to restrict the theoretical concept of species to particular time levels (whose ‘duration’ will have to be defined) and to speak of phyletic lineages in the time dimension. A separate taxonomy for such lineages outside the Linnaean system of genera and species should be designed.

Species taxa based upon morphological analyses of fossil specimens may or may not correlate with reproductive communities (biological species). In morphologically well differentiated groups, species probably often refer to taxa below the level of biospecies, whereas in morphologically (osteologically) uniform groups such as, e.g., salamanders or certain groups of songbirds, a fossil species probably comprises a group of closely allied biological species.

In a very perceptive early remark, Neumayr (1889: 67) was insisting that the concept of species, as derived from observations of extant faunas, cannot be applied to phyletic lineages. "However", he continued, "if we take a particular (form) by itself without regard to the other members of its lineage and consider only its relations to contemporary organisms, then indeed this form is a good species. As soon as we take into consideration the entire phyletic lineage of which this form is a part, nothing exists which would correspond to a species. The species concept cannot be applied when reasonably complete paleontological material is available and must disappear from the realm of paleontology." Similarly, Simpson (1943: 171) stated: "Clearly a species as a subdivision of a temporal, or vertical, succession is quite a diffent thing from a species as a spatial, or horizontal, unit and cannot be defined in the same way. The difference is so great and, to a thoughtful paleozoologist, so obvious that it is proper to doubt whether such subdivisions should be called species and whether vertical classification should not proceed on an entirely different plan from the basically and historically horizontal Linnean system. So far none of the varied proposals for non-Linnean arrangement and nomenclature has been widely accepted and none seems promising at present."

Despite this early advice (see also Sylvester-Bradley 1956, Simpson 1961, Reif 1984) palaeontologists and cladists continue to discuss 'species' concepts that refer to differently delimited portions of phyletic lineages. Hopefully, further discussions will lead to a clarification of the issues involved.

An early attempt at analyzing 'vertical' genealogical relations among extant taxa at the level of subspecies and species was made by Reinig (1938a,b, 1939a,b), who wisely used a new terminology for the entities he delimited in his studies (contrasting them to Rensch's terms of monotypic and polytypic species). Considering the postglacial expansion of birds from postulated glacial refugia in the Holarctic Region, Reinig traced genealogical units ("Sippe") on the basis of his analyses of geographical character gradients (determining character polarity on the basis of the assumed direction of range expansion from the refugia). A genealogical unit embraces all those populations ("Kleinsippe", geographical subspecies) that are morphologically and geographically differentiated (diagnosable) and "which are interrelated in such a way that each single group can be derived phylogenetically with the aid of morphological characteristics and historical and chorological knowledge from the group immediately adjacent to it" in the direction of the Pleistocene refuge area, where the expansion of the genealogical unit presumably had started (Reinig 1939a: 23). He felt that many species of the Palaearctic fauna may not represent evolutionary communities, i.e. be monophyletic in a cladistic sense, and explained that his term 'Sippe' (genealogical unit) has no definite taxonomic rank lying outside the customary categories of species and subspecies. Eller (1939, 1940) applied Reinig's methods to an analysis of the genealogy of geographical subspecies of the *Papilio machaon* group of butterflies. Reinig did not, however, provide examples at the species level to illustrate the differences between his approach and the application of the concept of biospecies. Non-hybridizing genealogical units in contact (paraspecies) are designated also by Reinig with a Linnaean binomen (species). He preferred to combine allopatric genealogical entities in loosely defined Formenkreise *sensu* Kleinschmidt. Reinig's rather unfortunate terminology of "Sippen" was 'preoccupied' by botanical usage and by the 19th-century natural philosopher Lorenz Oken who had suggested to replace the term genus by "Sippe".

More recent analyses of the 'vertical' (historical) relationships of groups of reptile populations at the infraspecific level are those of Böhme (1978) and Thorpe (1984).

Species limits under the cladistic species concept range from fairly wide (Hennig 1966, Willmann 1983, 1985, 1986) to narrow (Cracraft 1983, McKitrick & Zink 1988). Hennig and many other cladists delimit extant species basically following the criteria of the multidimensional species category. These latter systematists consider it inappropriate to enquire whether species are monophyletic, paraphyletic or polyphyletic, claiming that these terms apply only to groups of species (but see De Queiroz & Donoghue 1988, McKitrick & Zink 1988 and further discussions in *Cladistics* 5, 1989 and 6, 1990). On the other hand, cladists applying narrow species limits under the concept of the phylogenetic species (Cracraft 1983) assign species status to any population that is morphologically diagnosable (which basically renders this concept, in an operational, not theoretical, sense comparable to the monotypic morphological concept of 19th-century systematists). These cladists are concerned that paraphyletic and polyphyletic taxa may be ranked as species if medium-wide and wide species limits are applied.

A biological species becomes paraphyletic when a daughter species originated through 'budding' (Fig. 3); e.g., a derivative population of a widespread mainland species may have reached species status on a nearby island. However, this speciation event had no effect on the parental biospecies (no. 3, Fig. 3) on the mainland from which neospecies 4 has budded off. The mainland species (no. 3) is real in the sense that it represents a biological unit characterized by close genetic-reproductive and ecological relations among its component subspecies taxa. Traditionally, such biological clusters have been designated as 'species'. They would be in need of another categorical name if the term 'species' was to be transferred to the lower taxonomic level of the basic component morphotaxa (subspecies). The cladistic analyses schematically illustrated in Fig. 3 (if feasible at that infraspecific level) yield relevant phylogenetic ('vertical') and biogeographical data on the origin of the various groups of taxa. However, transfer and application of the term 'species' to phylogenetic lineages within biospecies would confuse the issue. Cracraft (1983) and other cladists suggest that each of the 9 lineages illustrated in Fig. 3 should be considered as species, regardless of their forming 4 separate clusters through genetic cohesion and intergradation.

Several large sample studies of birds should be undertaken to determine approximately what percentage of biospecies are monophyletic entities and how many species are paraphyletic or polyphyletic taxa.

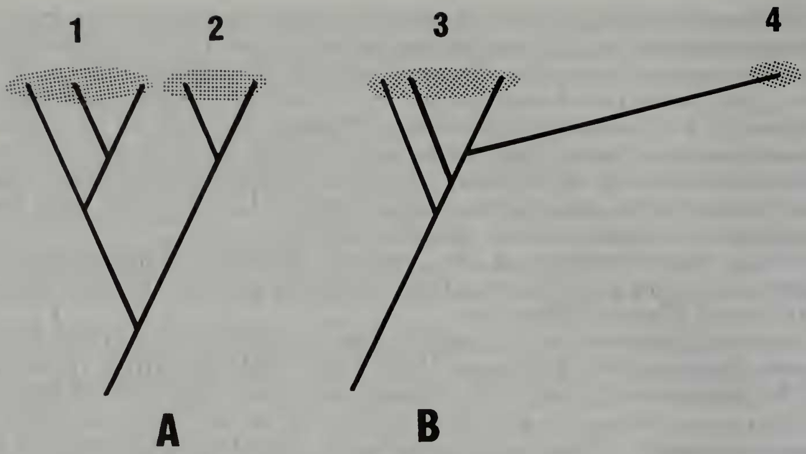

Figure 3. Speciation through splitting (A) and budding (B) resulting in monophyletic biospecies 1 and 2 (consisting of 3 and 2 subspecies, respectively) and paraphyletic biospecies 3 (3 subspecies). Species 4 which budded off from species 3 is monotypic and may demonstrate its species status by occurring sympatrically with some or all subspecies of species 3. Shading indicates genetic cohesion and intergradation of subspecies along contact zones.

McKitrick & Zink (1988: 8) believe that "many if not most biological species probably are monophyletic" and Szalay & Bock (1991: 35) are of the opinion that probably "many species" are paraphyletic. It would indeed be an important task to analyze phylogenetic lineages at intraspecific levels in the world's avifauna in order to understand the phylogenetic relations of as many component taxa of biological species as possible and to study their biogeographical history.

Geneflow among contiguous conspecific populations may prevent a meaningful cladistic analysis for many such taxa to be carried out. It would appear, therefore, that, among infraspecific entities, acceptable results of cladistic studies can be expected only for allopatric taxa and, in the case of contiguous populations, when these represent well differentiated (mega)subspecies characterized by morphological traits that can be assumed are not easily affected by geneflow.

THE CHANGING NUMBERS OF BIRD SPECIES

Because of the different opinions among ornithologists as to the circumscription of species taxa, i.e. their application of different taxonomic species categories, a higher or lower number of bird species has been recognized at all times. These different counts refer to the birds of the world as a whole, of a large continental region or an archipelago, though not to the number of bird species at a single locality which, of course, coincides under the various taxonomic categories of species discussed. Ornithologists applying a narrow morphological species category in taxonomy arrived at high numbers of species which, during the last century, were rapidly increasing due to the continuous discovery and description of new forms made known through numerous scientific expeditions (Fig. 4). On the other hand, ornithologists following the

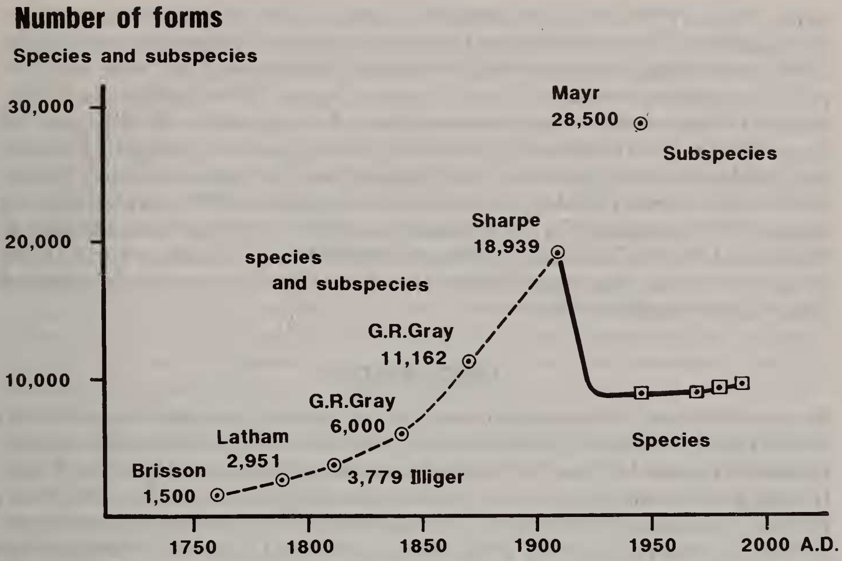

Figure 4. Increase of the number of species and subspecies of birds known during the last 250 years. Application of the multidimensional species concept (under the theoretical concept of the biological species) shortly after the end of the 19th century caused a conspicuous decrease in the number of species taxa recognized, a development which was stopped during the late 1920s when geographically representative biospecies were discovered. Data are from Stresemann (1975), Bock & Farrand (1980) and Sibley & Monroe (1990).

principles of the Gloger-Middendorff school in Europe and of the Bairdian school in North America recognized considerably fewer species; others arrived at an intermediate number. Whereas in North America the situation regarding intermediate species limits remained quite stable into the 20th century, a narrow monotypic species category was applied by the leading museum ornithologists in Europe toward the end of the 19th century resulting in the recognition of high numbers of species taxa, mainly through the influence of the authoritative 'Catalogue of the Birds in the British Museum' (27 volumes, 1874–1898). This trend culminated when R. B. Sharpe published his 'A Hand-list of the Genera and Species of Birds' (1899–1909) recognizing 18,939 species (many of which represent allospecies and subspecies).

During the following 20 years, the situation reversed itself entirely. Numerous Linnaean morphospecies were reinterpreted as subspecies and combined in more widely conceived biological species taxa. The result was a precipitous decline in the number of species recognized (Fig. 4). Several authors went too far in 'lumping' geographically representative forms into species units. This trend was eventually halted by warning voices from North America (e.g. Ridgway 1924, Swarth 1931, Chapin 1932, Stone 1935, Grinnell 1935) and especially by Rensch's (1928, 1929) emphasis on the existence of closely related allopatric and parapatric species (together forming a superspecies). A period of moderate stability regarding species numbers followed during the late 1930s and early 1940s when Mayr (1946: 68) estimated the total number of known birds to be 8616 species. A gentle increase of species numbers began during the late 1940s when many geographically isolated representatives were reinterpreted as species and combined in superspecies. This 'quiet revolution' (Mayr 1980b) at the microtaxonomic level during the last 30–40 years led to a continuous increase in the number of bird species, only slightly boosted by the discovery of genuine new biospecies (153 species from 1938 to 1985—Vuilleumier & Mayr 1987): Bock & Farrand (1980) counted a world total of 9021 species (3747 nonpasserines, 5274 passerines) and Sibley & Monroe (1990) 9672 species (3960 nonpasserines, 5712 passerines). In the latter species list, superspecies are indicated to give a measure of ecological units in the world's avifauna.

DISCUSSION

A consideration of reproductive communities (biospecies) refers to 'horizontal' relationships of extant populations or of contemporary populations at particular time levels in the geological past. On the other hand, tracing evolutionary descent of populations refers to a study of 'vertical' phyletic lineages (not 'species') through time. This contrasting and complementary way of looking at the 'horizontal' and 'vertical' relationships of taxa is reminiscent of a fundamental distinction made by several biologists and philosophers of the late 18th century, although details of these schemes are not directly comparable.

G. L. de Buffon distinguished from after 1740 a 'real' (physical) ordering of concepts and an 'abstract' ordering, thus viewing the taxonomic problem, in the first case, in terms of history and genealogy and, in the second case, in terms of morphology and character resemblance. He understood the different category levels—species, genera, orders, etc.—in 2 ways, in one as 'abstract' entities of reason, and in the other as grounded in the succession of real time and space in the Leibnizian understanding of those concepts (Sloan 1979: 117). Somewhat later, 1775–1788, Immanuel Kant distinguished in a similar way horizontal, a-temporal *Naturbeschreibung* (description of nature) and vertical, temporal *Naturgeschichte* (history of nature). Both Buffon and Kant related the recognition of natural species to the historical unity of the stem dividing animals according to genealogy (with reference to reproduction) rather than on the basis of morphological character resemblance (logical or morphological species of Linnaean taxonomy). All animals which generate fertile young with each other belong to a physical species.

Buffon's concepts, as clarified and to some extent reinterpreted by Kant, were made, in 1796, by Christoph Girtanner the basis of an appeal for a new and generalized research programme in natural history: an inquiry into the temporal and genealogical relations of life was to be separated from the traditional taxonomic and morphological approach. However, Girtanner's proposal had little impact on contemporary systematic studies and the writings of influential authors. Johann Blumenbach during the 1790s emphasized morphological aspects (the *habitus*) and Carl Illiger in 1800 shifted ambiguously from the domain of Naturgeschichte to Naturbeschreibung (Sloan 1979: 143).

My review of theoretical species concepts and of narrow to wide taxonomic species categories as applied by ornithologists over the last 200 years indicates that the basic questions, as in other branches of science as well, had been formulated already by the early pioneers (Haffer 1990). Throughout the 19th century, controversies persisted among ornithologists advocating wide or narrow species limits based on interbreeding and morphological considerations, respectively. The 'horizontal' biological species concept (Mayr 1942) was accepted by a majority of systematists during the first half of this century. Explicitly genealogical considerations were introduced later by Willy Hennig (1950, 1966) in his historical analyses of species populations based on cladistic methods.

Application of a narrowly defined taxonomic species category led systematists to assign species status to the smallest diagnosable taxa and, in this way, to emphasize nature's diversity at low taxonomic levels; whereas the delimitation of wide biogeographical species taxa (superspecies and independent species) stresses the recognition of ecological units in the world's fauna (Bock & Farrand 1980). The definition of the biological species category takes into consideration the most significant microtaxonomic event, i.e. the attainment of genetic isolation by a group of populations; consequently, biospecies are delimited as genetically closed reproductive communities at intermediate levels of microtaxonomic differentiation.

A practical application of a narrow, morphologically defined taxonomic species category (e.g. the cladistic concept of 'phylogenetic species') would result in an enormously increased number of taxonomic species compared to that currently recognized under the multidimensional taxonomic species category. On the other hand, application of the category of the wide biogeographical species would lead to a reduction of the number of presently recognized species. The approximately 9600 known extant biological species of birds (Sibley & Monroe 1990), according to 2 estimates, form 5000–6000 biogeographical species (Bock & Farrand 1980) or 7000 ± 200 biogeographical species (Mayr 1980b). These current issues in systematic ornithology represent the latest reformulation of ancient questions which have been discussed intensively throughout the nineteenth century and before.

All levels of differentiation at which species limits have been proposed are biologically significant. It will be advisable, therefore, that these stages of increased microtaxonomic differentiation are taken into consideration by identifying and listing the subspecies groups (megasubspecies, i.e. 'phylogenetic species'), the biological species and the biogeographical species in the world's avifaunas. In this way, the conceptual relations among these taxonomic categories and their component taxa may be studied, and the various entities may be used in analyses of the biogeographical and phylogenetic history as well as the ecological divergence of genera and families of birds.

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Summary

The theoretical concept of the biological species and the multidimensional species category, as currently applied by a majority of ornithologists and by many other biologists, replaced the typological-morphological species concept during the first half of this century and became a central tenet of the synthetic theory of evolution. The concept of biospecies is a 'horizontal' concept referring to contemporary reproductive communities at any particular period, e.g. the Recent period or any other time level of the geological past. Historical 'species' concepts as applied by cladists and palaeontologists refer to artificially delimited portions of 'vertical' phyletic lineages for which the application of the term 'species' causes severe problems. Discussions would be simplified if the concept and term 'species' was to be restricted to cross sections of phyletic lineages at any time level and a separate taxonomy outside the Linnaean system of genera and species was to be conceived to deal with phyletic lineages. Under each of the theoretical species concepts, species taxa are assigned broadly to intermediate or narrowly defined taxonomic species categories.

Ornithologists of the 19th century applied morphological species concepts, emphasizing morphological character differences between species (rather than distinctness) and the fertility of conspecific individuals (rather than the isolation from non-conspecific populations). Nearly all leading museum ornithologists in 19th-century Europe delineated monotypic Linnaean species, whereas the explorer-naturalists of the Gloger-Middendorff school (including Pallas, Faber, Gloger, Nordmann, Middendorff, Schrenck, Radde, as well as Schlegel and Blasius) delimited widely circumscribed species taxa. Their researches in the vast territories of eastern Europe, Siberia and the Far East from the late 18th century to the 1880s and, in particular, their rich specimen material, demonstrated direct intergradation of many taxa (geographical varieties) of birds, thus revealing the conspecific nature of numerous narrowly conceived morphospecies previously described by museum workers. The ornithologists of the Gloger-Middendorff school also studied several conspicuous phenomena of geographical character variation in birds (and mammals) across Eurasia, especially plumage colouration (and pelage) and body size, but none of them was an evolutionist. They all adhered to a typological-creationist theoretical species concept. During the late 19th century, the museum specialists' taxonomic notion of narrow morphospecies dominated systematic ornithology in Europe, overtaking the work of the naturalists of the Gloger-Middendorff school, which fell into oblivion.

The ornithologists of the Bairdian school in North America (Baird, Coues, Allen, Ridgway) further developed the concept of subspecies after the 1850s and especially from the 1870s onward. Their views were fully in accord with Darwin's theories of evolution; thus they defined the subspecies in a somewhat simplified manner as 'nascent species'. These ornithologists were able to base their studies on collections of extensive specimen material which they had obtained during a series of exploring expeditions across the North American continent. Their studies led to the discovery of many aspects of both individual and geographic variation in birds.

There are interesting historical similarities between the coinciding taxonomic interpretations and the comparable application of fairly broad limits of morphospecies by the North American ornithologists and the earlier exploring ornithologists in Europe, arrived at independently by these research groups. The study of specimens in 'series' ('suites'), beginning with the naturalists of the Gloger-Middendorff school and, in particular, with the naturalists of the Bairdian school in North America, eventually led to the overcoming of the prevailing typological view of variation and the development of 'population thinking'.

Influenced by the work of Henry Seebohm in Britain and that of the North American ornithologists, Hartert in England and Kleinschmidt in Germany jointly succeeded in overcoming the strong opposition of the leading ornithologists in Europe during the 1890s and early 1900s and introduced a concept which soon developed into the biological species concept through the work of Stresemann, Rensch, and in particular, Ernst Mayr.

Hopefully, ornithologists will continue the study of taxa at low, intermediate and high levels of microtaxonomic differentiation and will identify the subspecies groups, biological species and the biogeographical species in the world's avifaunas. Cladistic analyses will provide historical ('vertical') overviews of phyletic lineages at different taxonomic levels.

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